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A TEXT-BOOK OF ZOOLOGY



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ZOOLOGY

SECTION XIII

PHYLUM CHORDATA.

THE Phylum Chordata comprises all the Vertebrate animals (Fishes, Amphibians, Reptiles, Birds, and Mammals) together with the Urochorda or Ascidians and the Adelochorda or Balanoglossus and its allies. The name Chordata is derived from one of the most important of the few but striking common features by which the members of this extensive phylum are united together—the possession either in the young condition or throughout life of a structure termed the *chorda dorsalis* or *notochord*. This is a cord of cells, typically developed from the endoderm, extending along the middle line on the dorsal side of the enteric cavity, and on the ventral side of the central nervous system. It becomes enclosed in a firm sheath, and forms an elastic supporting structure. In the Vertebrata (with the exception of Amphioxus and the Lampreys and Hag-fishes) it becomes in the adult replaced more or less completely by a segmented bony or cartilaginous axis —the spinal or vertebral column. Another nearly universal common feature of the Chordata is the perforation of the wall of the pharynx, either in the embryonic or larval condition only, or throughout life, by a system of clefts—the branchial clefts: and a third is the almost universal presence at all stages, or only in the larva, of a cavity or system of cavities, the *neurocœle*, in the interior of the central nervous system.

SUB-PHYLUM AND CLASS I.—ADELOCHORDA.

Until quite recently a single genus, *Balanoglossus*, was the only known representative of a class to which the name *Enteropneusta* was applied. There seems reason to believe, however, that two remarkable deep-sea animals—*Rhabdopleura* and *Cephalodiscus*— though not close allies of Balanoglossus, may yet be sufficiently nearly related to it to justify their being placed in the same class.

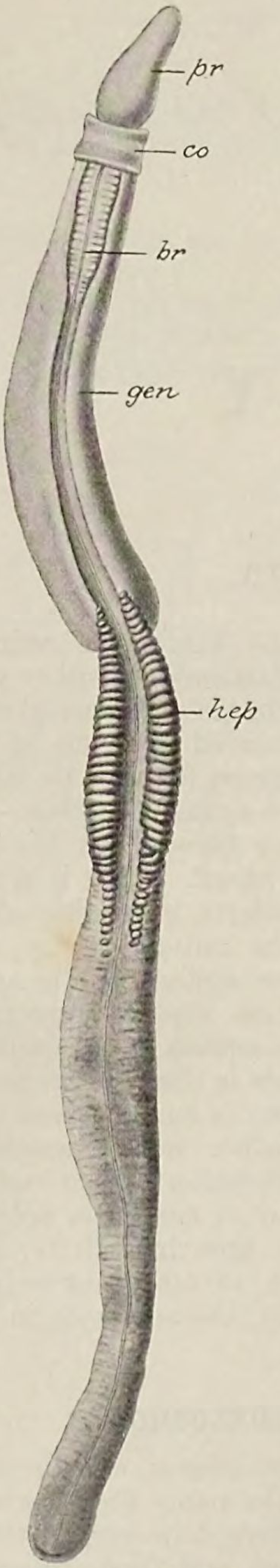


FIG. 664. — **Balanoglossus.** Entire animal. *br.* branchial region; *co.* collar; *gen.* genital ridges; *hep.* prominences formed by hepatic cœca; *pr.* proboscis. (After Spengel.)

External Characters. — Balanoglossus (Fig. 664) is a soft-bodied, cylindrical, worm-like animal, the surface of which is uniformly ciliated. It is divisible into three regions; in front there is a large club-shaped hollow organ—the *proboscis* (*pr.*); immediately behind the proboscis and encircling its base is a prominent fold—the *collar* (*co.*); the third region or *trunk* is long and nearly cylindrical, but somewhat depressed.

Balanoglossus lives in the sea, burrowing in sand or mud by means of its proboscis. Numerous glands in the integument secrete a viscid matter to which grains of sand adhere in such a way as to form a fragile temporary tube. The proboscis (Fig. 665, *prob.*) has muscular walls; its cavity opens on the exterior usually by a single minute aperture—the *proboscis pore* (*prb. po.*)—rarely by two. Its narrow posterior part or "neck" is strengthened by a layer of cartilage-like or *chondroid* tissue, which supports the blood-vessels. The collar is also muscular, and contains one cavity or two (right and left) separated from one another by dorsal and ventral mesenteries, and completely cut off from the proboscis cavity. The collar cavity and also that of the proboscis are crossed by numerous strands of connective tissue of a spongy character. The collar cavity communicates with the exterior by a pair of *collar pores* —ciliated tubes leading into the first gill-slit or first gill-pouch.

On the dorsal surface of the anterior part of the trunk is a double row of small slits—the *gill-slits* (Fig. 664, *br.*)—each row situated in a longitudinal furrow; these slits increase in number throughout life. The most anterior are in some species overlapped by a posterior prolongation of the collar called the *operculum*. A pair of longi-

tudinal ridges—the *genital ridges* (*gen.*)—not recognisable in some species, extend throughout a considerable part of the length of the body both behind and in the region of the gill-slits (*branchial region*); these are formed by the internally situated gonads. Behind the branchial region are two rows of prominences (*hep.*) formed by the hepatic cœca. The trunk is irregularly ringed, this ringing, which is entirely superficial and does not correspond to an internal segmentation, being most strongly marked behind. The cœlome of the trunk is divided into two lateral closed cavities by a vertical partition (dorsal and ventral mesenteries).

Digestive Organs.—The mouth (Fig. 665, *mo.*) is situated ventrally at the base of the proboscis, within the collar. Into the dorsal half of the anterior portion of the alimentary canal open the internal gill openings. Each of these is in the form of a long narrow U, the two limbs separated by a narrow process—the *tongue*—which contains a prolongation of the body-cavity. The gill-pouches are supported by a chitinoid skeleton consisting of a number of separate parts. Each of these consists of a dorsal basal portion and three long narrow lamellæ, a median and two lateral; the median which is bifurcate at the end, lies in the septum or interval between two adjoining gill-sacs; the two lateral lie in the two neighbouring tongues. In some species a number of slender transverse rods—the *synapticulæ*—connect together the tongues and the adjoining septa.

The posterior part of the alimentary canal is a nearly straight tube with, in its middle part, paired *hepatic cœca*, which bulge outwards in the series of external prominences already mentioned. Posteriorly it terminates in an anal aperture situated at the posterior extremity of the body. Throughout its length it lies between the dorsal and ventral divisions of the vertical partition, which act as mesenteries.

Skeleton.—In front the dorsal wall of the anterior portion of the alimentary canal gives off a diverticulum (*div.*), the lumen of which extends nearly to the anterior end. This diverticulum consists of epithelium with gland cells and of a sort of retiform connective tissue; it has been supposed to be homologous with the notochord of the typical Chordata. In close relation with this on its ventral surface is the proboscis-skeleton (*prob. skel.*) which consists of a median part, of an hour-glass shape, with a tooth-shaped process, bifurcating behind into two flattened bars which lie in the anterior region of the collar and support the opening into the lumen of the diverticulum.

There is a **blood-vascular system** with dorsal and ventral longitudinal trunks. The dorsal vessel (*dors. v.*) lies above the notochord, and ends in front in a sinus situated in the anterior part of the collar and the neck of the proboscis. From the posterior part of the sinus is given off a vessel which bifurcates to

supply the proboscis. In communication with the sinus are a number of vessels of a bilateral plexus—the *glomerulus*—situated at the anterior end of the alimentary diverticulum. From the posterior end of each half of the glomerulus there passes backwards an efferent vessel which breaks up into a plexus; the two plexuses unite ventrally to form a median ventral plexus continuous behind with the ventral vessel. The dorsal sinus, having no definite walls

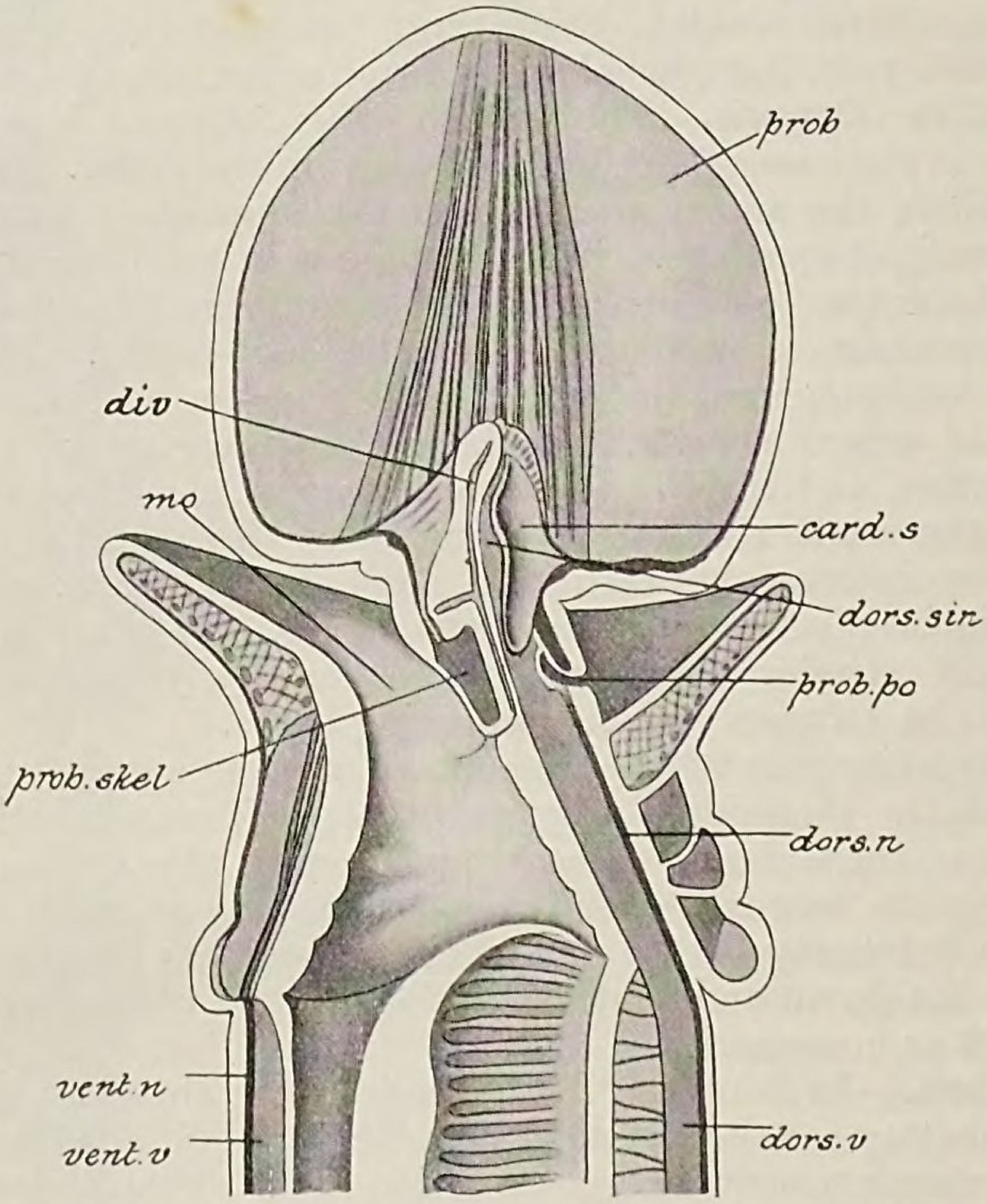


FIG. 665.—**Balanoglossus**. Diagrammatic sagittal action of anterior end. *card. s.* cardiac sac; *div.* diverticulum (supposed notochord); *dors. n.* dorsal nerve strand; *dors. sin.* dorsal sinus; *dors. v.* dorsal vessel; *mo.* mouth; *prob.* proboscis; *prob.po.* proboscis pore; *prob. skel.* proboscis skeleton; *vent. n.* ventral nerve strand; *vent. v.* ventral vessel. (After Spengel.)

is not contractile; but a closed sac, the *cardiac sac* (*card. s.*), derived from the heart of the larva and situated on the dorsal side of the sinus, has a muscular ventral wall by the contractions of which the blood may be propelled.

The **nervous system** consists of dorsal and ventral strands (*dors. n., vent. n.*) which extend throughout the length of the body. These are merely thickenings of a layer of nerve-fibres which extends over the entire body below the epidermis—the thickening being enclosed on both sides by a layer of cells which passes into

the epidermis. Here and there are giant nerve-cells. The part of the dorsal strand which lies in the collar (collar cord) is detached from the epidermis; it contains a larger number of the giant nerve-cells than the rest; in some species it contains a canal, the neurocœle, opening in front and behind; in others a closed canal; in most a number of separate cavities. Between the collar and the trunk the dorsal and ventral strands are connected by a ring-like thickening. There are no organs of special sense; but some cells of the epidermis on certain parts of the proboscis and on the anterior edge of the collar seem to be of the character of sensory cells.

Reproductive Organs.—The sexes are separate and often differ in colour; the ovaries and testes are saccular organs arranged in a double row along the branchial region of the trunk and further back; they open on the exterior by a series of pores.

The course of the **development** (Fig. 666) differs in different species. In some it is comparatively direct; in others there is a metamorphosis. Impregnation is external. Segmentation is complete and fairly regular; resulting in the formation of a blastula which is at first rounded, then flattened. On one side of the flattened blastula an invagination takes place. The embryo at this stage is covered with short cilia, with a ring of stronger cilia. The aperture of invagination becomes closed up, and the ectoderm and endoderm become completely separate. The embryo becomes elongated and a transverse groove (*gr.*) appears (*A*): the mouth is formed by an invagination in the position of the groove. The anus is developed in the position formerly occupied by the blastopore. Before the mouth appears there are formed two diverticula of the archenteron which become completely separated off, their cavities subsequently giving rise to the cavities of the proboscis and of the collar and the body cavity of the trunk. By the appearance of a second transverse groove (*B*) the body of the embryo becomes divided into three parts—an anterior, a middle and a posterior—these

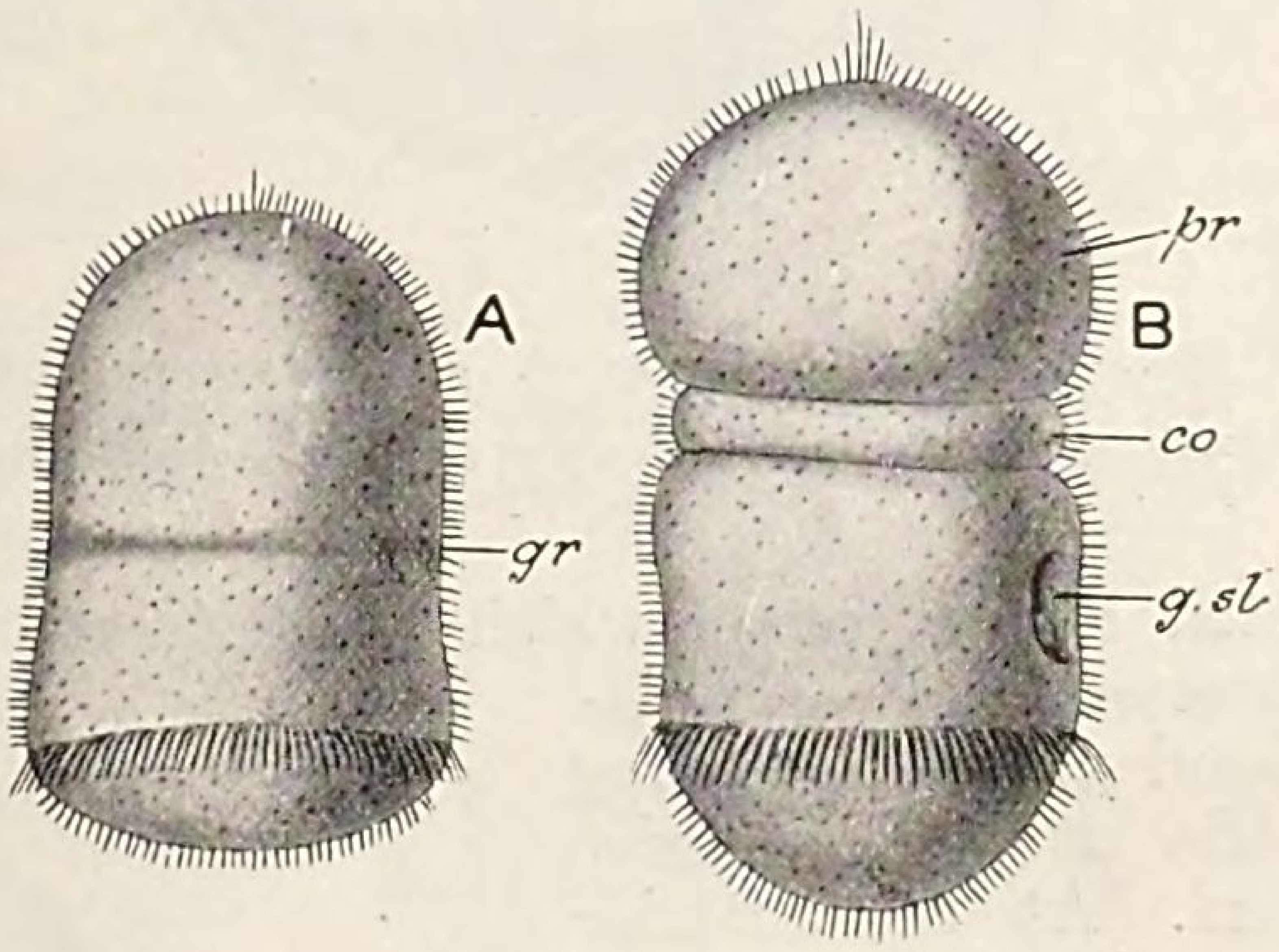


Fig. 666.—Development of **Balanoglossus.** *A*, stage of the formation of the first groove (*gr.*). *B*, stage in which the second groove has appeared, and the first gill slit has become developed; *co.* collar; *g. sl.* gill slit; *pr.* proboscis. (After Bateson.)

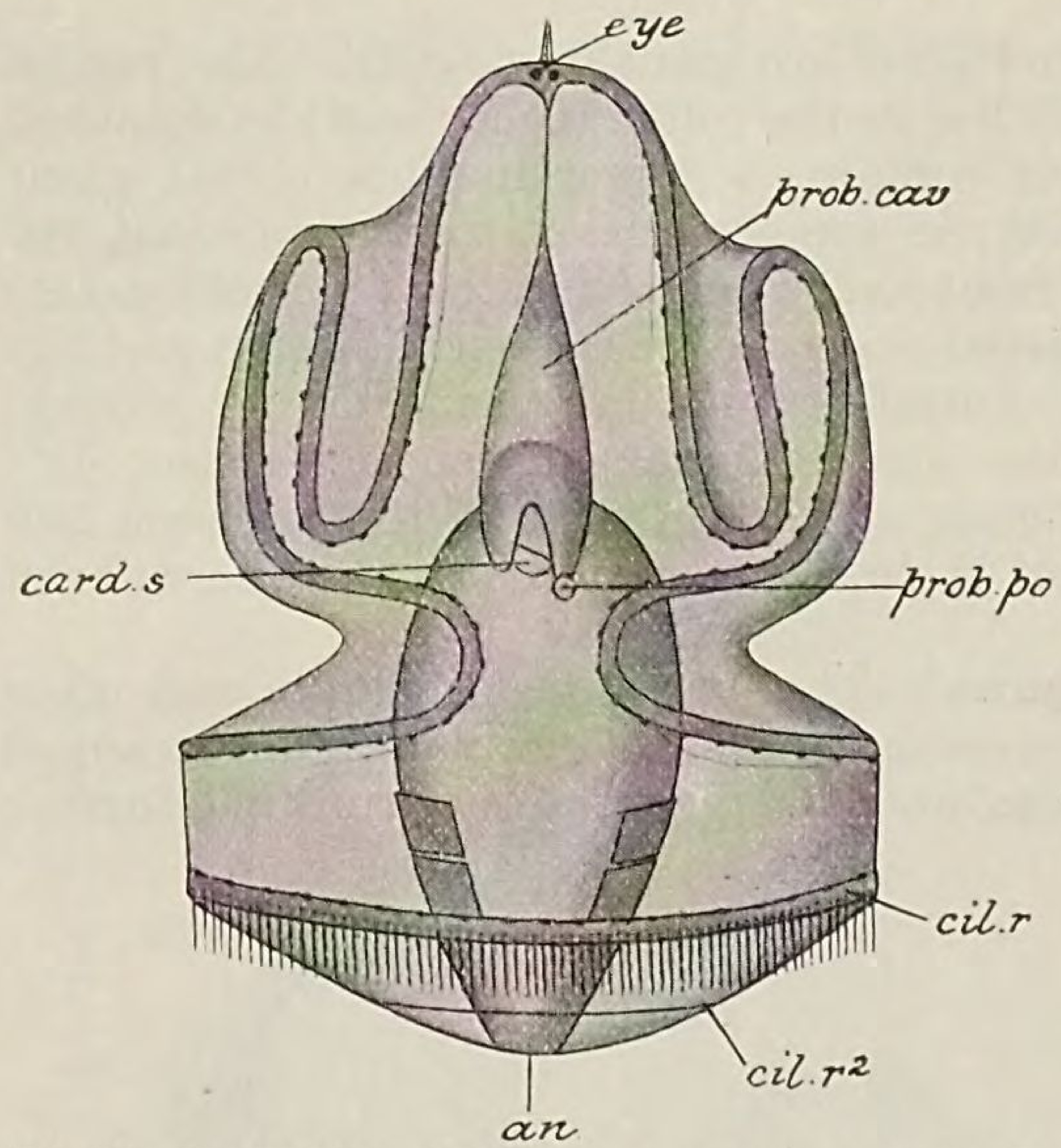


Fig. 667.—**Tornaria.** Dorsal view. *an.* anus; *card. s.* cardiac sac; *cil. r.* post-oral ciliated band; *cil. r²*. proberior ciliated ring; *eye*, eye-spots on apical plate; *prob. cav.* proboscis cavity; *prob. po.* proboscis pore. (After Spengel.)

being the beginnings respectively of the proboscis, the collar and the trunk. The branchial region becomes marked off by the appearance of a pair of apertures—the first pair of branchial slits (*g. sl.*)—and other pairs subsequently develop behind these.

In the species that undergo a metamorphosis the embryo assumes a larval form termed *Tornaria*. This (Figs. 667 and 668) is somewhat like an Echinoderm larva, with a pair of ciliated bands, one of which is considered præ-oral, and the other post-oral, and an independent circlet of strong cilia at the posterior end. At the anterior end, in the middle of the præ-oral lobe, is an ectodermal thickening—the *apical plate*—containing nerve-cells and eye-spots and, like the apical plate of a trochosphere, constituting the nerve-centre of the larva: this disappears in the adult. There is a short alimentary canal with mouth and anus. The ciliated bands become lost; an outgrowth is formed to give rise to the proboscis, and a constriction separates

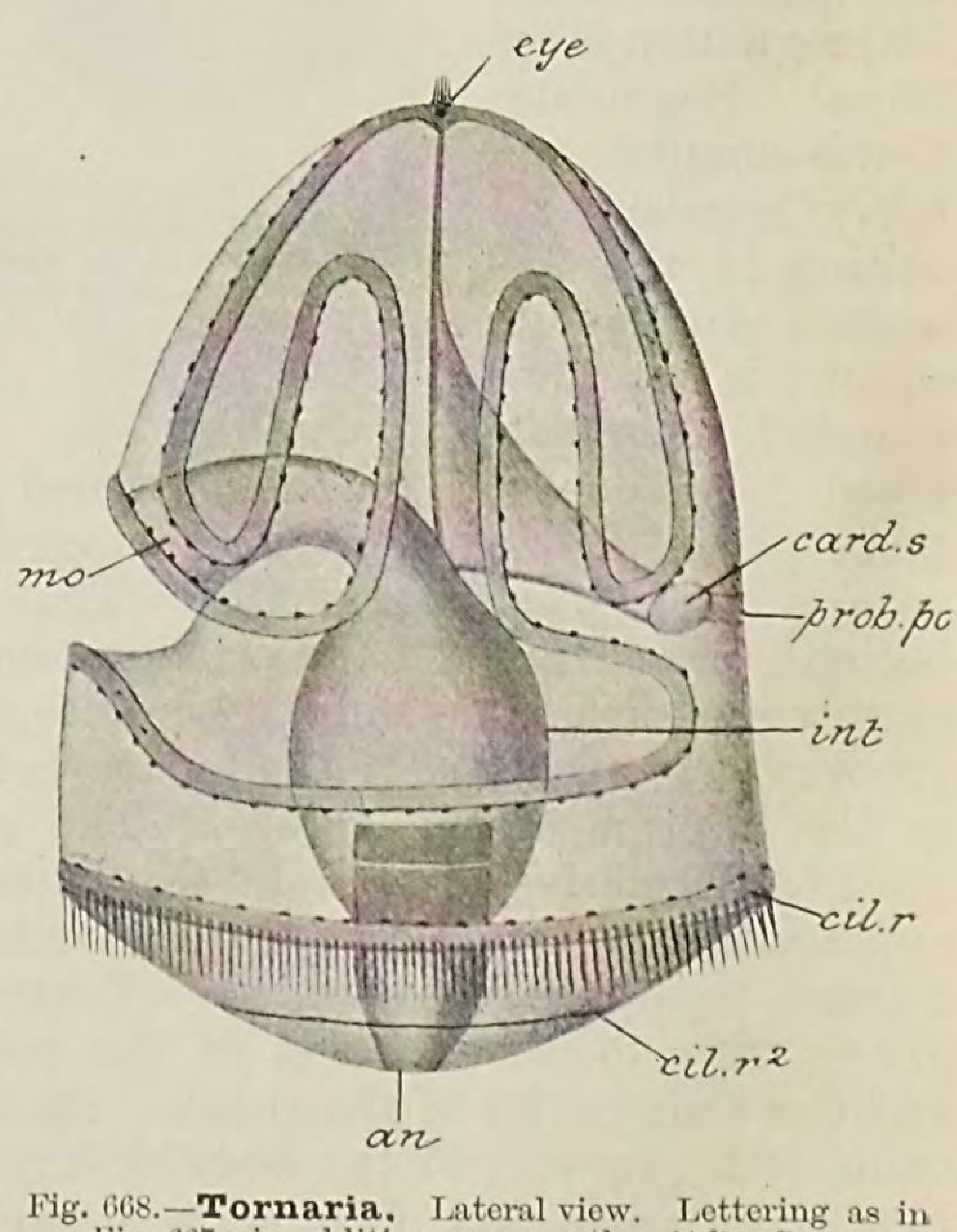


Fig. 668.—**Tornaria.** Lateral view. Lettering as in Fig. 667; in addition, *mo.* mouth. (After Spengel.

it from the collar; the hinder part becomes elongated and narrow to form the body of the worm; a series of perforations from the exterior give rise to the branchial pouches. A band of thickened epithelium has been described as developed on the wall of the œsophagus and has been supposed to correspond to the structure termed *endostyle* to be subsequently met with in the Tunicata (p. 14). The collar-fold is formed by the separating off of the deeper portion of the ectoderm along the middle line: or, in other species, by a sinking down of the whole thickness of the layer, which becomes cut off to form a medullary plate with its edges overlapped by the ectoderm.



FIG. 669.—**Cephalodiscus.** Gelatinous investment. (After McIntosh.)

Usually associated with Balanoglossus are two aberrant animals — *Cephalodiscus* and *Rhabdopleura* — formerly regarded as Polyozoa. These both resemble Balanoglossus in having the body divided into three parts or regions—a *proboscis,* with a proboscis cavity, a *collar* with a collar-cavity communicating with the exterior by a pair of collar-pores, and a *trunk* with two distinct lateral cavities; and in the presence of a structure resembling a notochord with the same relations to the nervous system as in Balanoglossus. They both differ from Balanoglossus in having the alimentary canal bent on itself so that the anal opening is situated not far from the mouth; in the presence of tentacles arising from the collar; and in the comparatively small size of the proboscis. Cephalodiscus, moreover, has only a single pair of apertures which may be regarded as representing the gill-slits; while in Rhabdopleura such openings are entirely absent. Both forms occur in associations or colonies secreting a common case or investment. Both occur at considerable depths in the sea.

Cephalodiscus has an investment (Fig. 669) in the form of a

branching gelatinous structure, which is beset with numerous short filiform processes, and contains a number of cavities occupied by zooids. The latter (Fig. 670) are not in organic continuity, so that though enclosed in a common investment

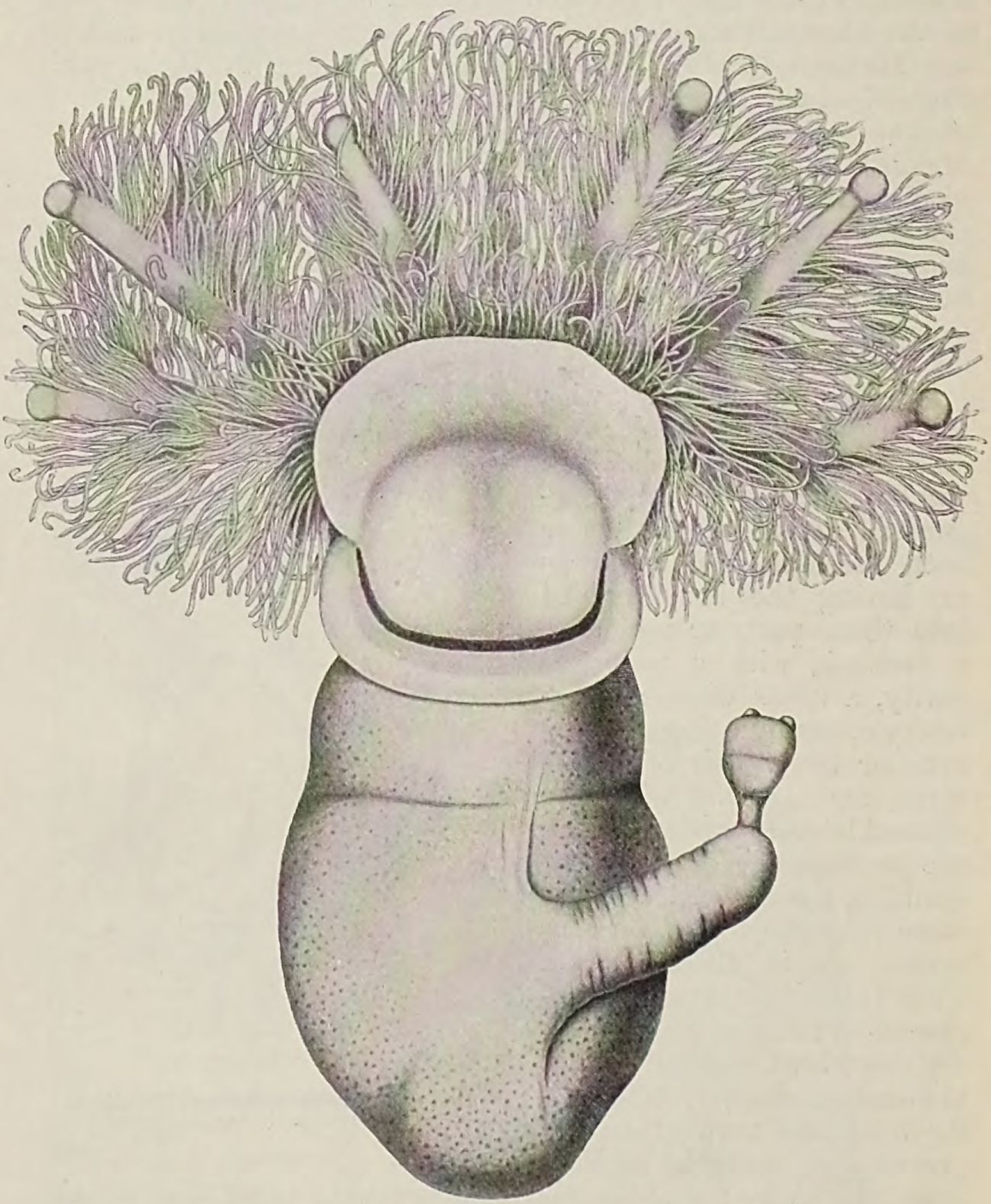


FIG. 670.—**Cephalodiscus.** Entire zooid. (After McIntosh.)

they do not form a colony in the sense in which the word is used of the Polyzoa or the Hydroid Zoophytes. They have this feature in common with such a colony that they multiply by the formation of buds; but these become detached before they

are mature. With the collar region are connected a series of twelve arms or tentacles, each beset with numerous very fine filaments and containing a prolongation of the collar cavity. The proboscis (Fig. 671, *ps.*) is a shield-shaped lobe overhanging the mouth; its cavity communicates with the exterior by two proboscis pores (*p.p*). The cavity of the collar communicates with the exterior by a pair of ciliated passages opening by the collar pores. Behind the collar region is on each side a small area in which the body-wall and that of the pharynx are coalescent; this area is usually, though

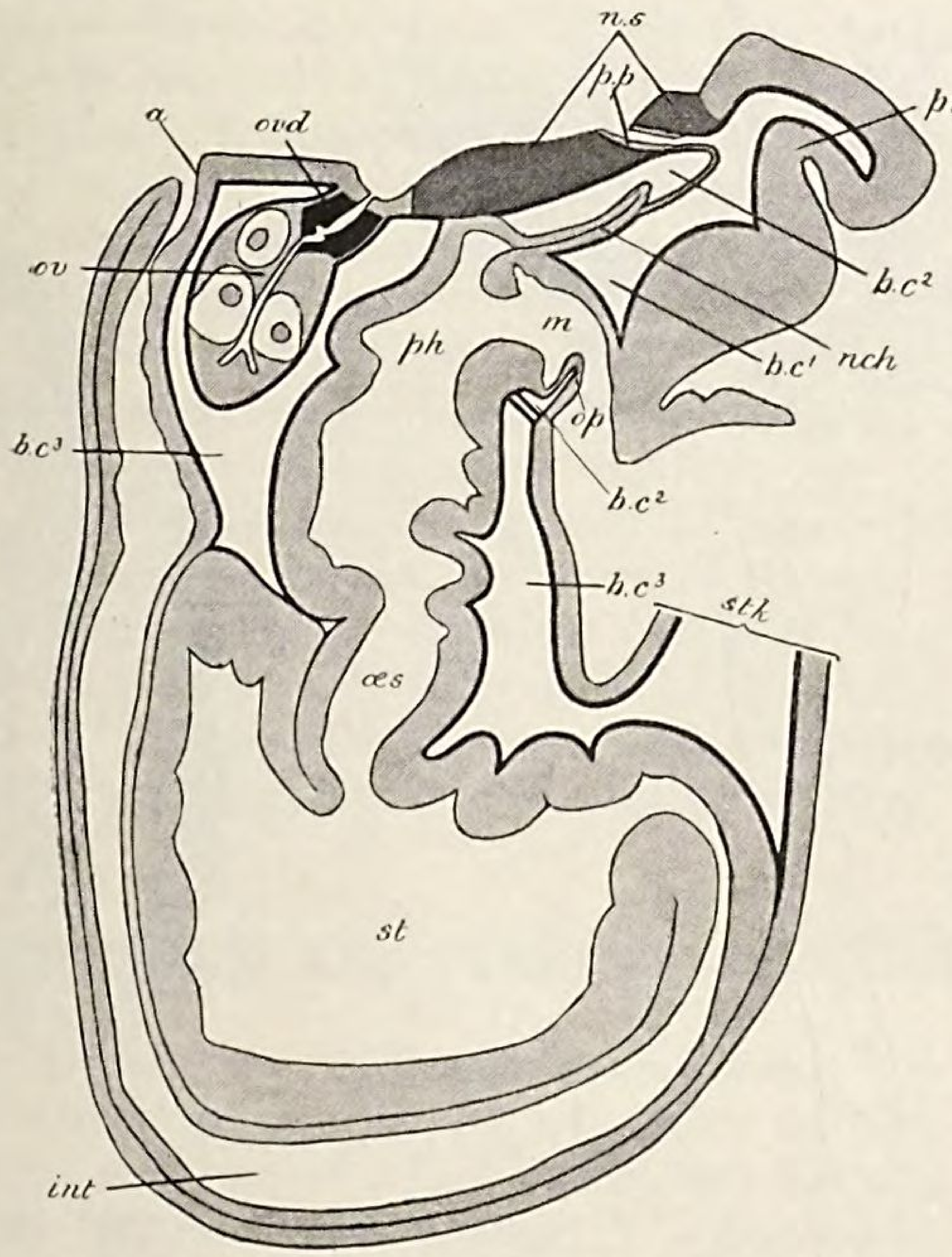


FIG. 671.—**Cephalodiscus.** Diagram of longitudinal section. *a.* anus; *bc*¹. column of proboscis; *bc*². cœlom of collar; *bc*³. cœlom of trunk; *int.* intestine; *nch.* supposed notochord; *n.s.* nerve-strand; *œs.* œsophagus; *ov.* ovary; *ovd.* oviduct; *ph.* pharnyx; *p.p.* proboscis pore; *ps.* proboscis; *st.* stomach; *stk.* stalk. (After Harmer.)

not always, perforated by an opening—the *gill-slit*. A nerve-strand containing nerve fibres and ganglion cells is situated on the dorsal side of the collar and is prolonged on to the dorsal surface of the proboscis and the dorsal surface of the arms. On the ventral side of this nerve-strand is a very slender cylindrical cellular cord (*nch.*) continuous behind with the epithelium of the pharynx: this is supposed to represent the diverticulum of Balanoglossus, and thus to be homologous with the notochord of the Chordata. The posterior end of the body is drawn out into a sort of stalk on which the buds are developed (Fig. 670). A pair of

ovaries (*ov.*) lie in the trunk cavity; and there is a pair of oviducts (*ovd.*) (originally supposed to be eyes) lined by elongated pigmented epithelium.

Rhabdopleura (Fig. 672) occurs in colonies of zooids organically connected together, and enclosed in, though not in organic continuity with, a system of branching membranous tubes. The

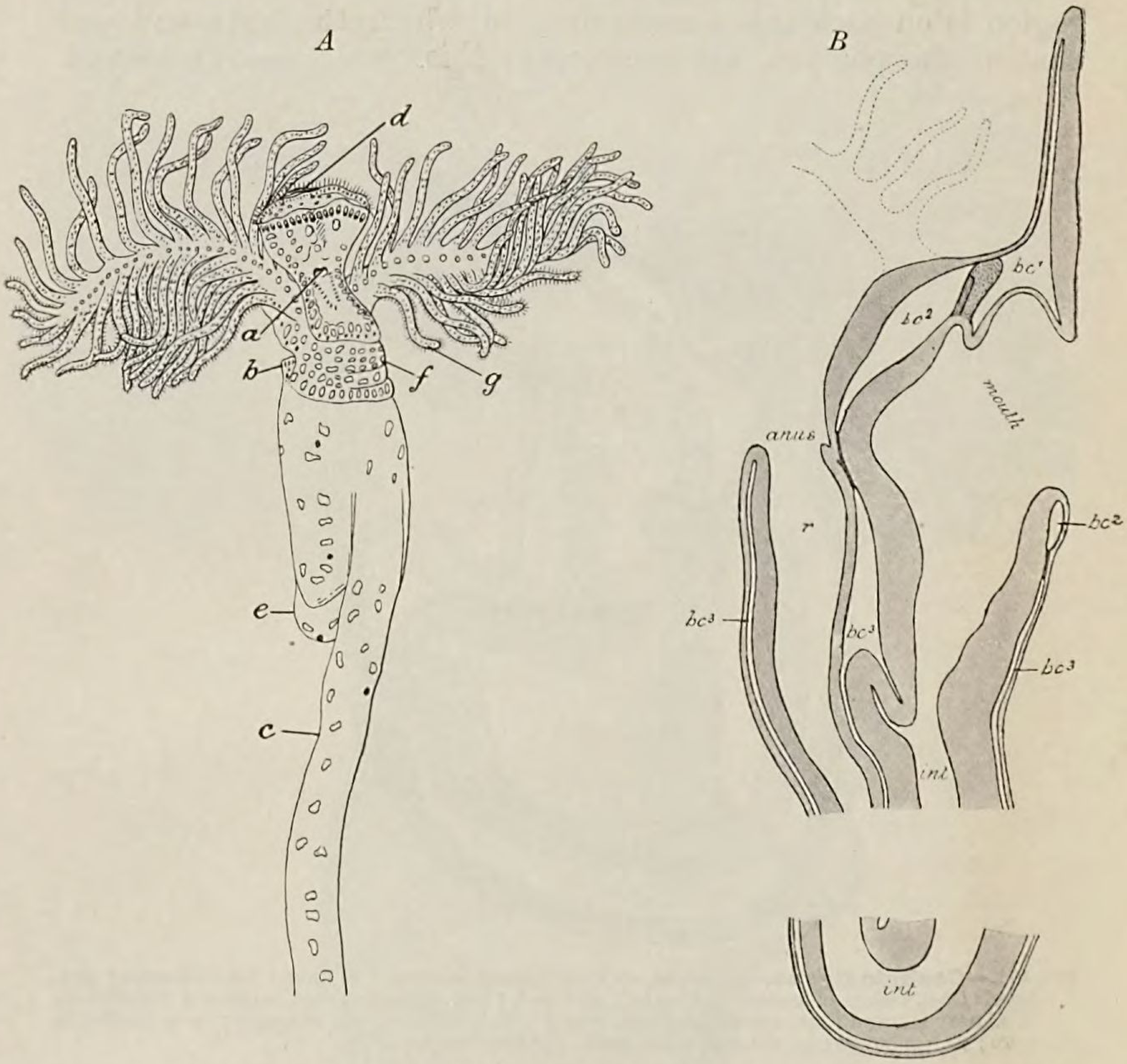


Fig. 672.—**Rhabdopleura.** *A*, Entire zooid. *a*, mouth; *b*, anus; *c*, stalk of zooid; *d*, proboscis; *e*, intestine; *f*, anterior region of trunk; *g*, one of the tentacles. (After Ray Lankester.) *B*, Diagrammatic longitudinal section a little to one side of the median line. *anus*, anus; bc^1. cœlome of proboscis; bc^2. cœlome of collar; between bc^1. and bc^2. is the diverticulum; bc^3. cœlome of trunk; *int*. intestine; *mouth*, mouth; *r*. rectum. (After Fowler.)

collar region bears a pair of arms or tentacles, each carrying a double row of slender filaments—the whole supported by a system of firm internal (cartilaginous?) rods. The "notochord" and the nervous system resemble those of Cephalodiscus. A single testis has been found, opening on the exterior by a pore situated near the anus. The female reproductive organs have not been discovered.

Affinities.—The inclusion of the Adelochorda in the phylum Chordata is an arrangement the propriety of which is not universally admitted, and is carried out here partly to obviate the inconvenience of erecting the class into a separate phylum. On the whole, however, there seems to be sufficient evidence for the view that, if not the existing representatives of ancestral Chordates, they are at least a greatly modified branch, taking its origin from the base of the Chordate tree. The presence of the presumed rudimentary representative of a notochord and of the gill-slits seems to point in this direction. It should, however, be stated that by some of those zoologists by whom the members of this group have been most closely studied, their chordate affinities are altogether denied. If the Adelochorda are primitive Chordates the fact is of special interest that among lower forms they show remarkable resemblances in some points to a phylum—that of the Echinodermata—which it has been the custom to place very low down in the invertebrate series. The Tornaria larva of Balanoglossus exhibits a striking likeness to an Echinopædium (vol. i. p. 396), and, though this likeness between the larvæ does not establish a near connection, it suggests, at least, that an alliance exists. Between Actinotrocha, the larva of Phoronis (vol. i. p. 330) and Tornaria there are some striking points of resemblance; and the discovery in the former of a pair of diverticula resembling the "notochord" of the Adelochorda lends support to the view that Phoronis is nearly related to the present group.

SUB-PHYLUM AND CLASS II.—UROCHORDA.

The Class Urochorda or Tunicata comprises the Ascidians or Sea-Squirts, which are familiar objects on every rocky sea-margin; together with a number of allied forms, the Salpæ and others, all marine and for the most part pelagic. The Urochorda are specially interesting because of the remarkable series of changes which they undergo in the course of their life-history. Some present us with as marked an alternation of generations as exists among so many lower forms; and in most there is a *retrogressive metamorphosis* almost, if not quite, as striking as that which has been described among the parasitic Copepoda or the Cirripedia. In by far the greater number of cases it would be quite impossible by the study of the adult animal alone to guess at its relationship with the Chordata; its affinities with that phylum are only detected when the life-history is followed out; the notochord and other higher structures becoming lost in the later stages of the metamorphosis. Multiplication by budding, so common in the lower groups of Invertebrata, but exceptional or absent in the higher, is of very general occurrence in the Urochorda.

1. Example of the Class—The Ascidian or Sea-Squirt (*Ascidia*).

Sea-squirts are familiar objects on rocky sea-shores, where they occur, often in large associations, adhering firmly to the surface of the rock. When touched the Ascidian ejects with considerable force two fine jets of sea-water, which are found to proceed from two apertures on its upper end. The shape of the Ascidian, however, can only be profitably studied in the case of specimens that are completely immersed in the sea-water, specimens not so immersed always undergoing contraction. In an uncontracted specimen (Fig. 673), the general shape is that of a short cylinder with a broad base by which it is fixed to the rock. The free end presents a large rounded aperture, and some little distance from it on one side is a second of similar character. The former aperture is termed the *oral*, the latter the *atrial*. A strong current of water will be noticed, by watching the movements of floating particles, to be flowing steadily in at the former and out of the latter. When the animal is removed from the water both apertures become narrowed, so as to be almost completely closed, by the contraction of sphincters of muscular fibres which surround them. At the same time the walls of the body contract, streams of water are forced out through the apertures, and the bulk becomes considerably reduced.



Fig. 673. — **Ascidia**, entire animal seen from the right-hand side. (After Herdman.)

Body-wall and Atrial Cavity.—The outer layer of the body-wall is composed of a tough translucent substance forming a thick *test* or *tunic* (Fig. 674, *test*). This proves when analysed to consist largely of the substance *cellulose*, which has already been referred to (vol. i. p. 14) as a characteristic component of the tissues of plants, and which is rare in its occurrence in the animal kingdom. The test of an Ascidian is frequently referred to as a cuticle, and it is a cuticle in the sense that it lies outside the ectoderm. The cells which form it, however, seem to be chiefly derived, not from the ectoderm, but from the underlying mesoderm, from which they migrate through the ectoderm to the outer surface. These formative cells of the test are to be found scattered through its substance. Running through it also are a number of branching tubes lined with cells, each terminal branch ending in a little bulb-like dilatation. The interior of each tube is divided into

two channels by a longitudinal septum which, however, does not completely divide the terminal bulb. Through these tubes (which are of the nature of blood-vessels) blood circulates, passing along one channel, through the terminal bulb, and back through the other channel.

When the test is divided (Fig. 674) the soft wall of the body or *mantle* (*mant.*), as it is termed, comes into view; and the body is

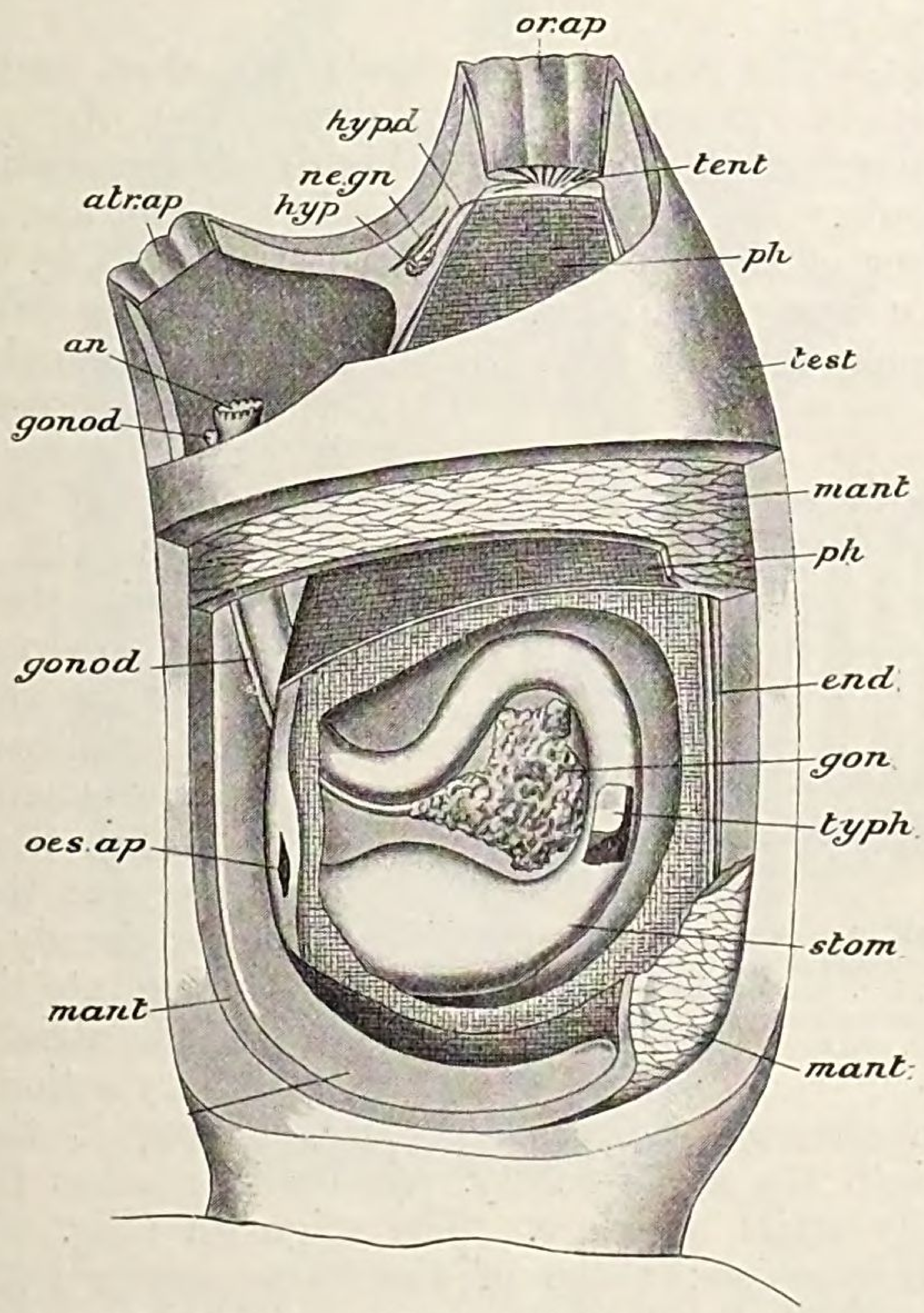


FIG. 674.—Dissection of **Ascidia** from the right-hand side. The greater part of the test and mantle has been removed from that side so as to bring into view the relations of these layers and of the internal cavities and the course of the alimentary canal, etc. *an.* anus; *atr. ap.* atrial aperture; *end.* endostyle; *gon.* gonad; *gonod.* gonoduct; *hyp.* hypophysis; *hyp. d.* duct of hypophysis; *mant.* mantle; *ne. gn.* nerve-ganglion; *œs. ap.* aperture of œsophagus; *or. ap.* oral aperture; *ph.* pharynx; *stom.* stomach; *tent.* tentacles; *test*, test. (After Herdman.)

found to be freely suspended within the test, attached firmly to the latter only round the oral and atrial apertures. The mantle (body-wall) consists of the ectoderm with underlying layers of connective tissue enclosing muscular fibres. It follows the general shape of the test, and at the two apertures is produced into short and wide tubular prolongations, which are known respectively as the *oral* and *atrial siphons* (Fig. 676, *or. siph. atr. siph.*). These are continuous at

their margins with the margins of the apertures of the test, and round the openings are the strong sphincter muscles by which closure is effected. In the rest of the mantle the muscular fibres are arranged in an irregular network, crossing one another in all directions. Within the body-wall is a cavity, the *atrial* or *peribranchial cavity* (*atr. cav.*), communicating with the exterior through the atrial aperture: this is not a cœlome, being formed by involution from the outer surface, and probably lined by a prolongation of the ectoderm.

Pharynx.—The oral aperture leads by a short and wide oral passage into a chamber of large dimensions, the *pharynx* or *branchial chamber* (*ph.*). This is a highly characteristic organ of the Urochorda. Its walls, which are thin and delicate, are pierced by a number of slit-like apertures, the *stigmata* (Fig. 676, *stigm.*) arranged in transverse rows. Through these the cavity of the pharynx communicates with the atrial or peribranchial cavity, which completely surrounds it except along one side. The edges of the stigmata are beset with numerous strong cilia, the action of which is to drive currents of water from the pharynx into the atrial cavity. It is to the movements of these cilia lining the stigmata that are due the currents of water already mentioned as flowing into the oral and out of the atrial apertures, the ciliary action drawing a current in through the oral aperture, driving it through the stigmata into the atrial cavity, whence it reaches the exterior through the atrial aperture. The stigmata (Fig. 675) are all vertical in position; those of the same row are placed close together, separated only by narrow vertical bars; neighbouring rows are separated by somewhat thicker horizontal bars; in all of these bars run blood-vessels.

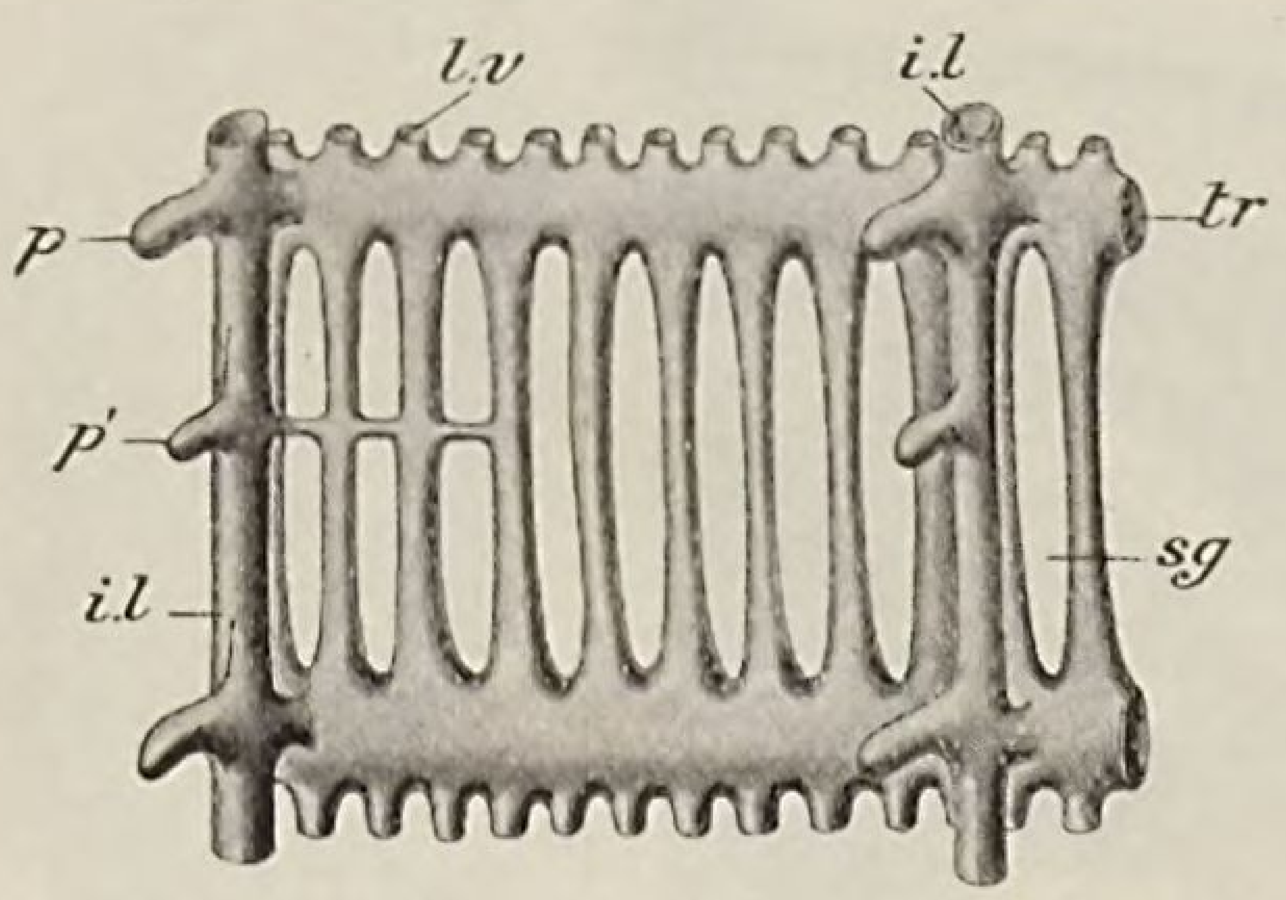


FIG. 675.—**Ascidia,** a single mesh of the branchial sac, seen from the inside. *i. l.* internal longitudinal bar; *l. v.* fine longitudinal vessel; *p. p'.* papillæ projecting inwards from the branchial bar; *sg.* stigma; *tr.* transverse vessel. (After Herdman.)

It has been already mentioned that the atrial cavity does not completely surround the pharynx on one side. This is owing to the fact that on the side in question, which is ventral in position, the wall of the pharynx is united with the mantle along the middle line (Fig. 677). Along the line of adhesion the inner surface of the pharynx presents a thickening in the form of a pair of longitudinal folds separated by a groove (*end.*). To this structure, consisting of the two ventral longitudinal folds with the groove between them, the term *endostyle* is applied. The cells covering the endostyle are large

cells of two kinds—*ciliated cells* and *gland cells*—the former beset at their free ends with cilia, the action of which is to drive floating particles that come within their influence outwards towards the oral aperture, the latter secreting and discharging a viscid mucous matter. Anteriorly the endostyle is continuous with a ciliated ridge which runs circularly round the anterior end of the pharynx.

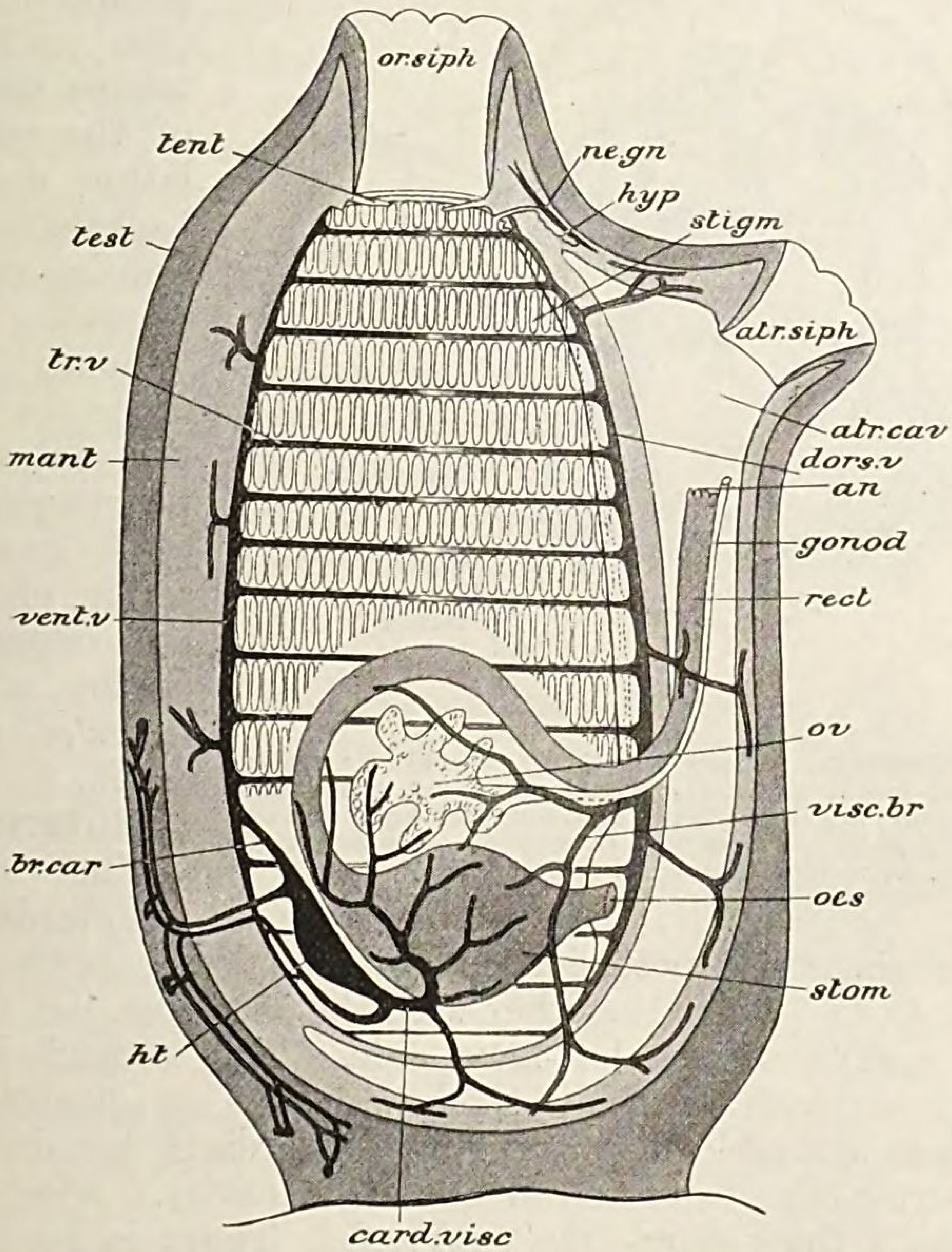


FIG. 676.—**Ascidia,** diagram of longitudinal section from the left-hand side, the test and mantle removed. *atr. cav.* atrial cavity; *atr. siph.* atrial siphon; *br. car.* branchio-cardiac vessel; *card. visc.* cardio-visceral vessel; *gonod.* gonoduct; *ht.* heart; *hyp.* hypophysis; *mant.* mantle; *n. gn.* nerve-ganglion; *œs.* œsophagus; *ov.* ovary; *rect.* rectum; *stig.* stigmata; *stom.* stomach; *tent.* tentacles; *test.* testis; *tr. v.* transverse vessel; *vent. v.* ventral vessel; *visc. br.* viscero-branchial vessel. (After Herdman.)

In front of this circular ridge, and running parallel with it, separated from it only by a narrow groove, is another ridge of similar character; these are termed the *peri-pharyngeal ridges;* the groove between them is the *peri-pharyngeal groove.* Dorsally, *i.e.* opposite the endostyle, the posterior peripharyngeal ridge passes into a median, much more prominent, longitudinal ridge, the *dorsal lamina* (*dors. lam.*), which runs along the middle of the dorsal surface of the pharynx to the opening of the œsophagus. The mucus secreted by

the gland cells of the endostyle forms viscid threads which entangle food-particles (microscopic organisms of various kinds); the cilia of its ciliated cells drive these forwards to the peribranchial groove, around which they pass to the dorsal lamina, and the cilia of the cells of the latter drive them backwards to the opening of the œsophagus.

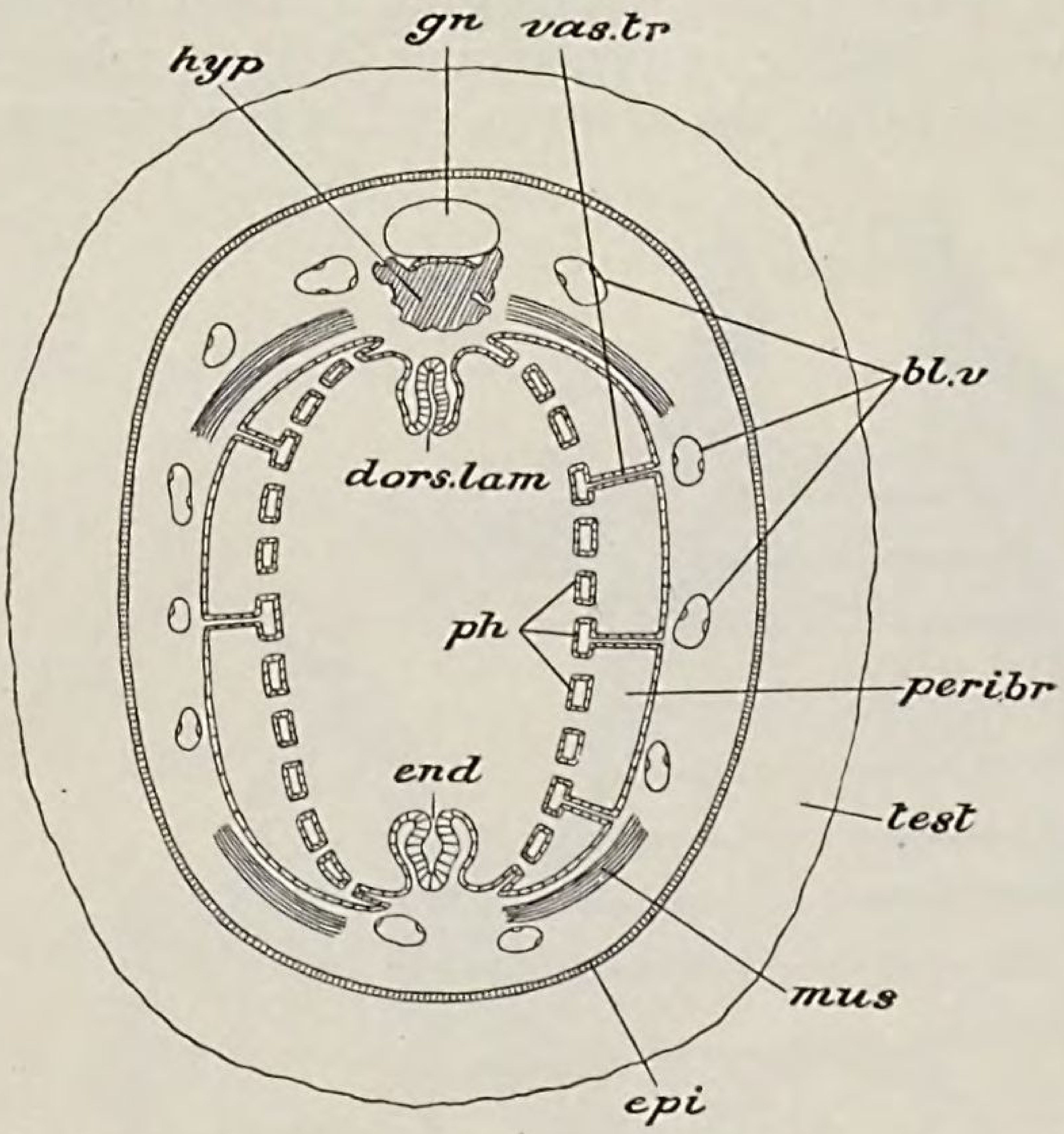


FIG. 677.—**Ascidia,** transverse section. *bl. v.* blood vessels; *dors. lam.* dorsal lamina; *epi.* epidermis; *end.* endostyle; *gn.* ganglion; *hyp.* hypophysis; *mus.* muscular layer of wall of body; *peribr.* peribranchial cavity; *ph.* pharynx; *test.* test; *vas. tr.* vascular trabeculæ. (After Julin.)

Some little distance in front of the anterior peripharyngeal ridge, at the inner or posterior end of the oral siphon, is a circlet of delicate *tentacles* (Fig. 674 *tent.*).

Enteric Canal.—The œsophagus (*œs.*) leads from the pharynx (near the posterior end of the dorsal lamina) to the stomach (*stom.*) which, together with the intestine, lies embedded in the mantle on the left-hand side. The stomach is a large fusiform sac with tolerably thick walls. The intestine is bent round into a double loop, and runs forwards to terminate in an anal aperture (*an.*) situated in the atrial cavity. Along its inner wall runs a thickening—the *typhlosole.* There is no liver; but the walls of the stomach are glandular, and a system of delicate tubules which ramify over the wall of the intestine is supposed to be of the nature of a digestive gland.

The Ascidian has a well-developed **blood system.** The heart (Fig. 676, *ht.*) is a simple muscular sac, situated near the stomach in a pericardium forming part of the primitive cœlome. Its mode of pulsation is very remarkable. The contractions are of a peristaltic character, and follow one another from one end of the heart to the other for a certain time; then follows a short pause, and, when the contractions begin again, they have the opposite direction. Thus the direction of the current of blood through the heart is reversed at regular intervals. At each end of the heart is given off a large vessel. That given off ventrally, the *branchio-cardiac vessel* (*br. car.*),

runs along the middle of the ventral side of the pharynx below (externally to) the endostyle, and gives off a number of branches which run along the bars between the rows of stigmata, and give off smaller branches passing between the stigmata of each row. The vessel given off from the dorsal end of the heart, the *cardio-visceral* (*card. visc.*), breaks up into branches which ramify over the surface of the alimentary canal and other organs. This system of visceral vessels or lacunæ opens into a large sinus, the *viscero-branchial* vessel, which runs along the middle of the dorsal wall of the pharynx externally to the dorsal lamina, and communicates with the dorsal ends of the series of transverse branchial vessels. In addition to these principal vessels there are numerous lacunæ extending everywhere throughout the body, and a number of branches, given off both from the branchio-cardiac and cardio-visceral vessels, ramify, as already stated, in the substance of the test. The direction of the circulation through the main vessels differs according to the direction of the heart's contractions. When the heart contracts in a dorso-ventral direction, the blood flows through the branchio-cardiac trunk to the ventral wall of the pharynx, and through the transverse vessels, after undergoing oxygenation in the finer branches between the stigmata, reaches the viscero-branchial vessel, by which it is carried to the system of visceral lacunæ, and from these back to the heart by the cardio-visceral vessel. When the contractions take the opposite direction, the course of this main current of the blood is reversed. The cavity of the heart and vessels is derived from the blastocœle or primary body-cavity of the embryo.

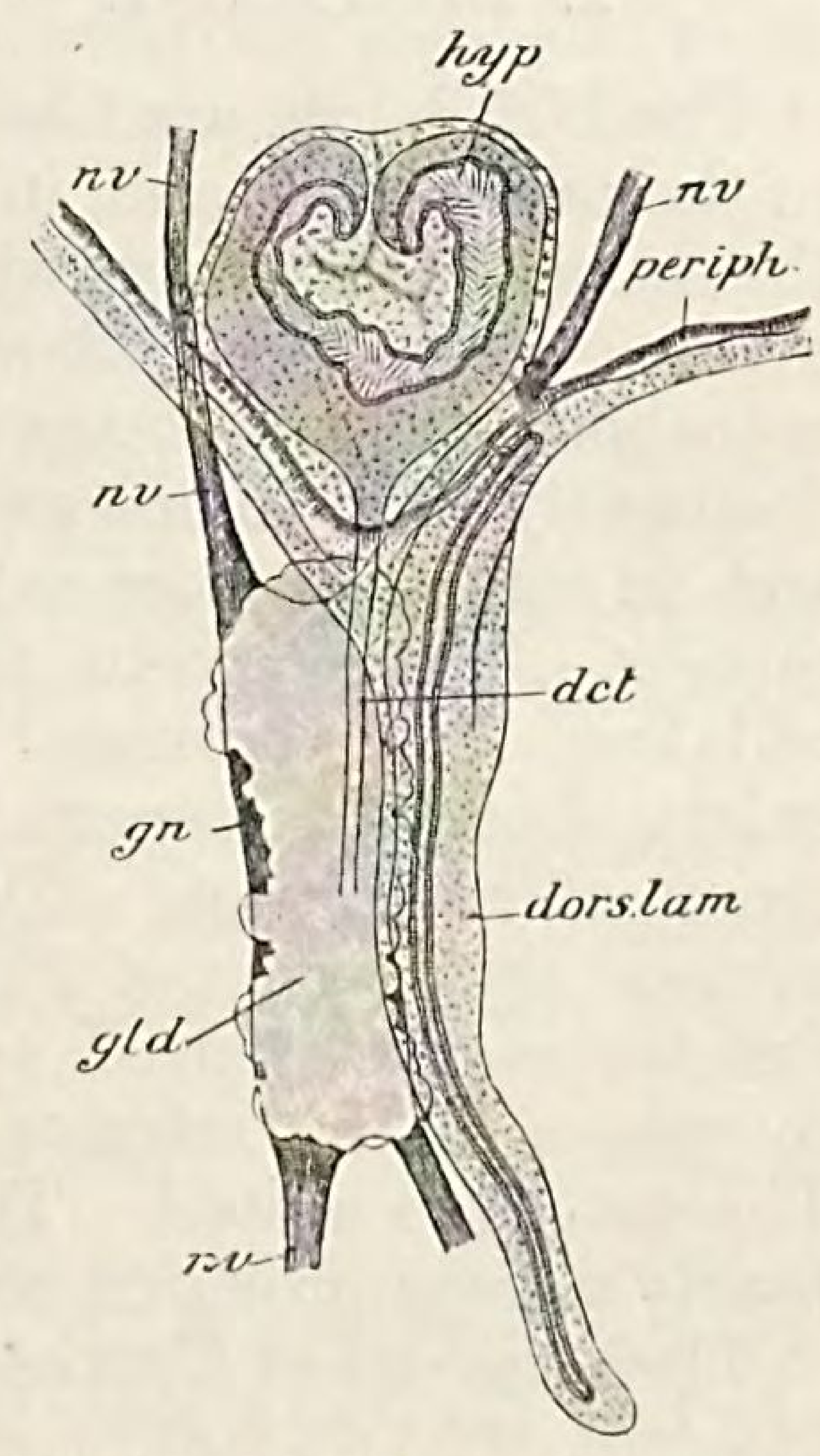


FIG. 678.—**Ascidia.** Hypophysis, nerve-ganglion and associated parts as seen from below. *dct.* duct of hypophysis; *dors. lam.* dorsal lamina; *gld.* subneural gland; *gn.* ganglion; *hyp.* hypophysis; *nv. nv.* nerves; *periph.* peripharyngeal band. (After Julin.)

The **nervous system** is of an extremely simple character. There is a single nerve-ganglion (Figs. 374 and 376, *ne. gn.*, and 378 *gn.*) which lies between the oral and atrial apertures, embedded in the mantle. This is elongated in the dorso-ventral direction, and gives off at each end nerves which pass to the various parts of the body.

Lying on the ventral side of the nerve-ganglion is a gland—the **sub-neural gland** (Figs. 674, 676, *hyp.*; Fig. 678, *gld.*)—which there is evidence for correlating with the *hypophysis* of the Craniata. A

duct (Fig. 678, *dct.*) runs forward from it and opens into the cavity of the pharynx; the termination of the duct is dilated, and this terminal dilatation is folded on itself in a complicated way to form a tubercle, the *dorsal tubercle*, which projects into the cavity of the pharynx.

The **excretory system** is represented by a single mass of clear vesicles, without a duct, lying in the second loop of the intestine. In the interior of these are found concretions containing uric acid.

Reproductive system.—The sexes are united. The ovary and the testis are closely united together, and lie on the left-hand side of the body in the intestinal loop. Each of them contains a a cavity which, like the pericardium and the cavities of the nephridial vesicles, forms a part of the original cœlome. Continuous with the cavity of each is a duct—oviduct or spermiduct, as the case may be—which opens into the atrial cavity close to the anus.

The **development** of the Ascidian is described below (p. 27).

2. Distinctive Characters and Classification.

The Urochorda are Chordata in which the notochord is confined to the tail region, and, in all but the Larvacea, is found only in the larva. The adults, which for the most part are retrogressively metamorphosed, in other respects besides the abortion of the notochord, are sometimes sessile, sometimes free and pelagic; they frequently form colonies (fixed or free) by a process of budding, and in some instances exhibit a well-marked alternation of generations. The body is enclosed in a test consisting largely of cellulose. The proximal part of the enteric canal (pharynx) is enlarged to form a spacious sac with perforated walls acting as an organ of respiration. There is a simple heart and a system of sinuses, the cavities of which are remains of the blastocœle. The cœlome is represented, apparently, only by the pericardium and by spaces in the interior of the gonads and of the renal organ. The sexes are united. The larva is always free-swimming, and is nearly always provided with a caudal appendage.

Three orders of Urochorda are recognised:—

Order 1.—Larvacea.

Free-swimming pelagic Tunicata with a caudal appendage, supported by a skeletal axis or notochord. The test is represented by a relatively large temporary envelope, the "house," formed with great rapidity as a secretion from the surface of the ectoderm and frequently thrown off and renewed. The pharynx has only two stigmata which lead directly to the exterior. There is no atrial

or peribranchial cavity. The principal nerve-ganglion gives off a nerve cord with ganglionic enlargements running to the tail, along the dorsal aspect of which it passes to the extremity. There is no reproduction by budding, and development takes place without metamorphosis.

This order contains only a single family, the *Appendiculariidæ*, with five genera, including *Appendicularia* and *Oikopleura*.

Order 2.—Thaliacea.

Free-swimming Tunicata, sometimes simple, sometimes colonial, never provided with a caudal appendage in the adult condition. The test is a permanent structure. The muscular fibres of the body-wall are arranged in complete or interrupted ring-like bands, or diffusely. The pharynx has either two large or many small stigmata leading into an atrial cavity which communicates with the exterior by the atrial aperture. There is usually an alternation of generations; there may or may not be a tailed larval stage.

Sub-Order a.—Cyclomyaria.

Thaliacea with a cask-shaped body, having the oral and atrial apertures at opposite ends, and surrounded by a series of complete rings of muscular fibres.

This sub-order contains only one family, the *Doliolidæ*, with the three genera, *Doliolum*, *Anchinia*, and *Dolchinia*.

Sub-Order b.—Hemimyaria.

Thaliacea with a more or less fusiform body, with sub-terminal oral and atrial apertures. The muscular fibres are arranged in bands which do not form complete rings.

There are two families—the *Salpidæ* and the *Octacnemidæ*—the latter comprising only the aberrant deep-sea genus *Octacnemus*, which seems to be fixed and not free-swimming like the rest of the order.

Sub-Order c.—Pyrosomata.

Thaliacea which reproduce by budding, so as to give rise to hollow cylindrical colonies, open at one or both ends, having the zooids embedded in the gelatinous wall in such a manner that the oral apertures open on the outer, the atrial on the inner, surface of the cylinder.

This sub-order comprises only one family, the *Pyrosomidæ*, with one genus, *Pyrosoma*.

Order 3.—Ascidiacea.

Mostly fixed Tunicata, either simple or forming colonies by a process of budding, and, in the adult condition, never provided

with a tail. The test is a permanent structure, usually of considerable thickness. The muscular fibres of the mantle (body-wall) are not arranged in annular bands. The pharynx is large, and its walls are perforated by numerous stigmata leading into a surrounding atrium or peri-branchial cavity, which communicates with the exterior by an atrial aperture. Many form colonies by a process of budding; and most undergo a metamorphosis, the larva being provided with a caudal appendage supported by a notochord similar to that of the Larvacea.

Sub-Order a.—Ascidiæ simplices.

Ascidians in which, when colonies are formed, the zooids are not embedded in a common gelatinous mass, but possess distinct tests of their own. They are nearly always permanently fixed and never free-swimming.

Including all the larger Ascidians or Sea-Squirts.

Sub-Order b.—Ascidiæ compositæ.

Fixed Ascidians which form colonies of zooids embedded in a common gelatinous material without separate tests.

This order includes *Botryllus*, *Amaræcium*, *Diazona*, and a number of other genera.

Systematic position of the Example.

The genus *Ascidia*, of which there are very many species, is a member of the family *Ascidiidæ* of the Ascidiæ simplices. The Ascidiidæ differ from the other families of simple Ascidians by the union of the following characters:—The body is usually sessile, rarely elevated on a peduncle. The oral aperture is usually 8-lobed and the atrial 6-lobed. The test is always of gelatinous or cartilaginous consistency. The wall of the pharynx is not folded; the tentacles are simple and filiform. The gonads are placed close to the intestine.

The genus Ascidia is characterised by having the oral and atrial apertures not close together, by the dorsal lamina being a continuous undivided fold, and by the ganglion and sub-neural gland being situated at a little distance from the dorsal tubercle.

3. General Organisation.

General Features.—*Appendicularia* (Fig. 679), which may be taken as an example of the Larvacea, is a minute transparent animal, in shape not unlike a tadpole, with a rounded body and a long tail-like appendage attached to the ventral side. At the extremity of the body most remote from the tail is the aperture

of the mouth. This leads into a tolerably wide pharynx (Fig. 680, *ph.*), in the ventral wall of which is an endostyle similar to that of the simple Ascidian, but comparatively short. Round the pharynx there run two bands covered with strong cilia—the *peripharyngeal bands.* On the ventral side of the pharynx there are two ciliated openings—the *stigmata* (*stig.*)—which communicate with the exterior by short passages—the *atrial canals*, situated on either side behind the anus. The axis of the tail is occupied by a cylindrical rod—the *notochord* (*noto.*).

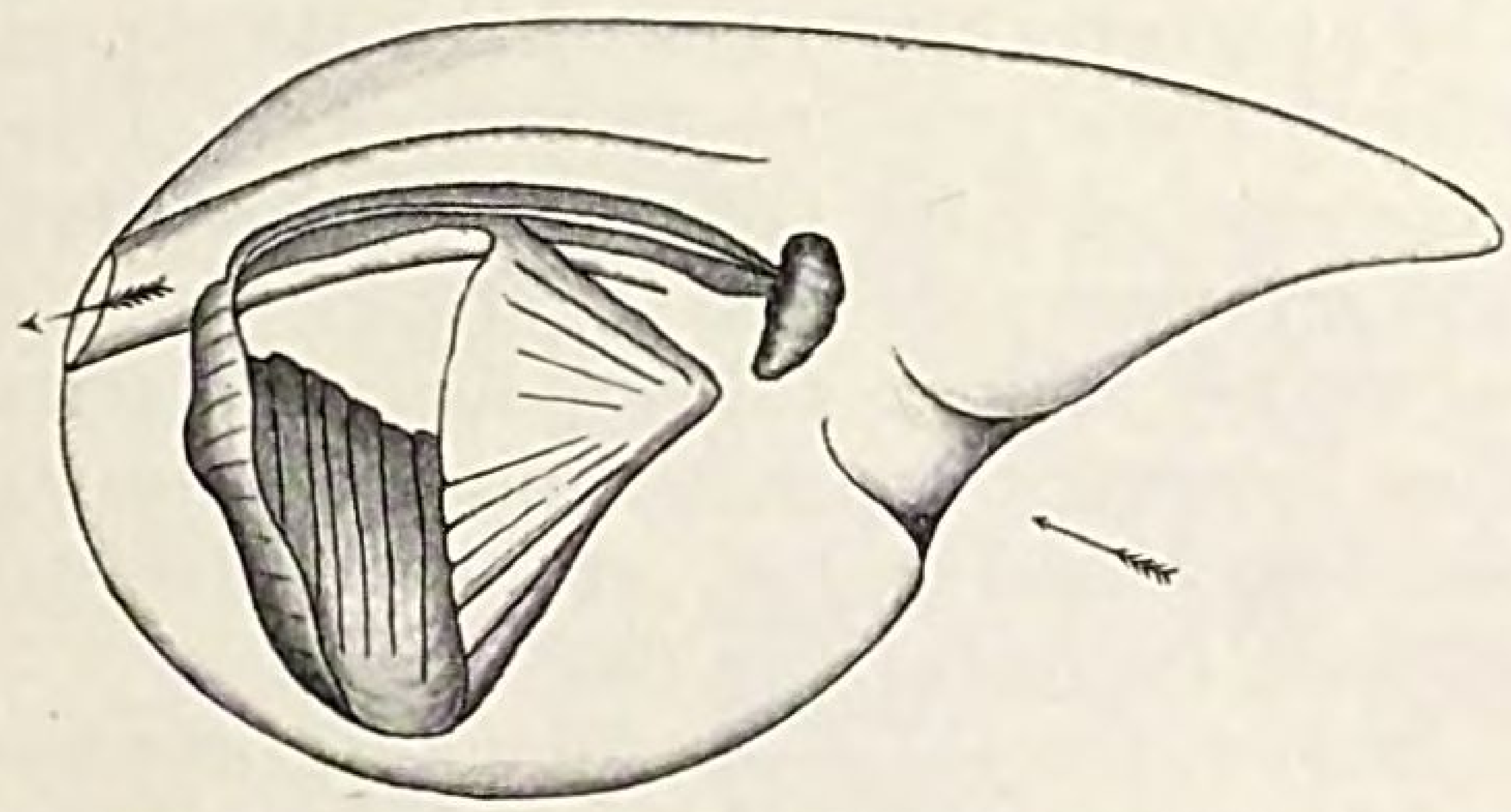


FIG. 679.—**Appendicularia** (**Oikopleura**) in "House." (From Herdman, after Fol.)

A remarkable peculiarity of *Appendicularia* is the power which it possesses of secreting from the surface a transparent envelope (Fig. 679) in the interior of which the animal can move freely. This structure—the *house* as it is called—is soon thrown off, and a new one developed in its stead. It represents the test or tunic of the simple Ascidian, though it does not appear to contain cellulose.

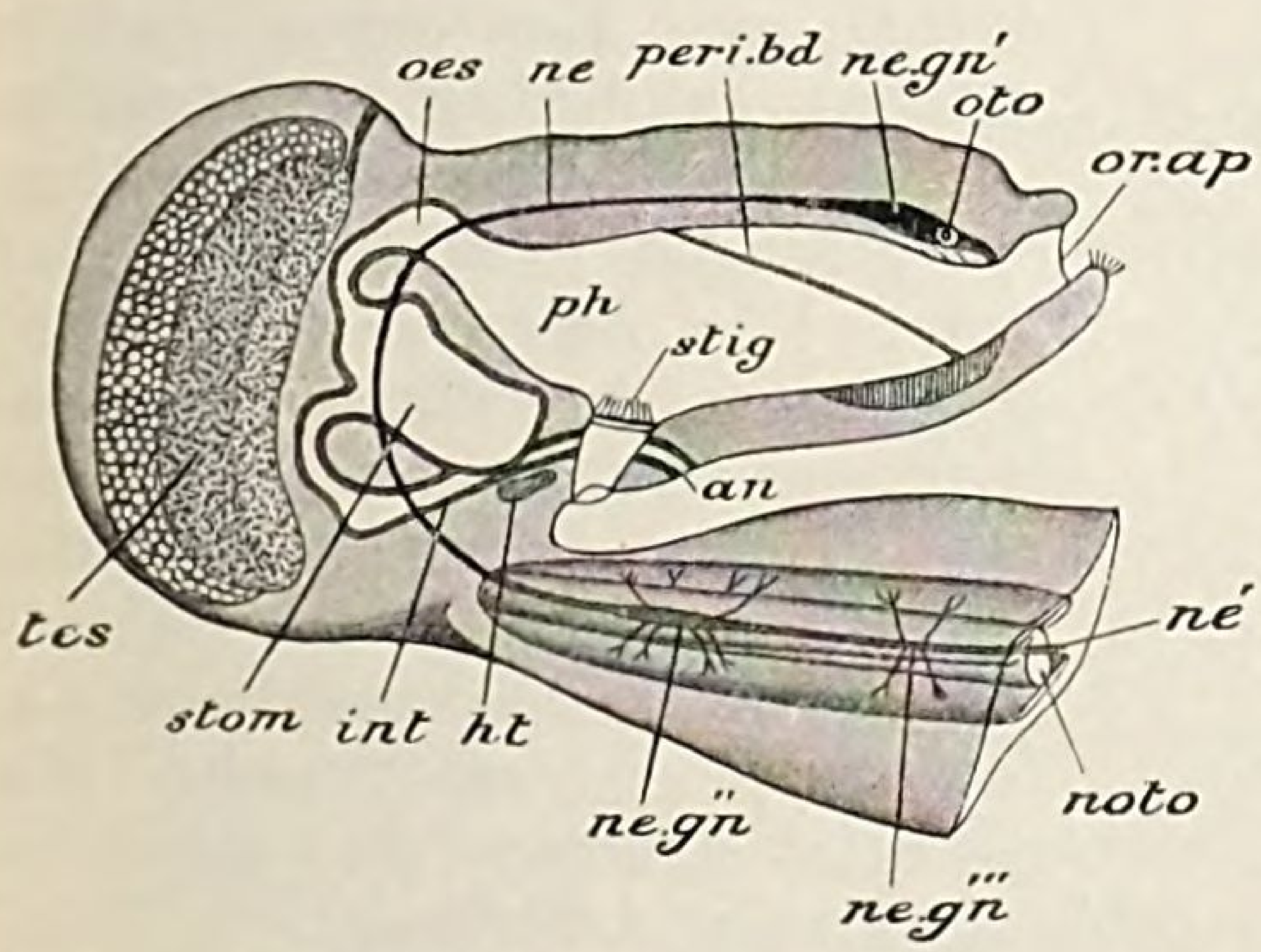


FIG. 680.—Diagram of **Appendicularia** from the right-hand side. *an.* anus; *ht.* heart; *int.* intestine; *ne.* nerve; *ne.'* caudal portion of nerve; *ne. gn.* principal nerve-ganglion; *ne. gn.' ne. gn.''* first two ganglia of nerve of tail; *noto.* notochord; *œs.* œsophagus; *or. ap.* oral aperture; *oto.* otocyst; *peri. bd.* peripharyngeal band; *ph.* pharynx; *tes.* testis; *stig.* one of the stigmata; *stom.* stomach. (After Herdman.)

Among the simple Ascidians there is a considerable degree of uniformity of structure, and there is not much that need be added here to the account given of the example. The shape varies a good deal: it is sometimes cylindrical, sometimes globular, sometimes compressed; usually sessile and attached by a broad base, often with root-like processes, but in other cases (*e.g. Boltenia*) elevated on a longer or shorter stalk. Most are solitary; but some multiply by budding, stolons being given off on which new zooids are developed. The test varies considerably in consistency, being some-

times almost gelatinous, transparent or translucent, sometimes tough and leathery, occasionally hardened by encrusting sand-grains or fragments of shells, or by spicules of carbonate of lime. The apertures always have the same position and relations, varying only in their relative prominence. The pharynx varies in its size as compared with the rest of the internal parts, in the position which it occupies with regard to the various parts of the alimentary canal, and in the number and arrangement of the stigmata. The tentacles are sometimes simple, sometimes compound; and the dorsal lamina may or may not be divided up into a system of lobes or *languets* (Fig. 682, *lang.*).

In the composite Ascidians, as mentioned in the summary, the zooids are embedded in a common gelatinous mass. The gelatinous colony thus formed is sometimes flat and encrusting, sometimes branched or lobed, sometimes elevated on a longer or shorter stalk. In certain forms (*Psammapilidium*) the gelatinous substance is hardened by the inclusion in it of numerous sand-grains. The arrangement of the zooids presents great differences. Sometimes they occur irregularly dotted over the entire surface without exhibiting any definite arrangement; sometimes they are arranged in rows or regular groups; in *Botryllus* (Fig. 681) they are arranged in star-shaped, radiating sets around a common cloacal chamber into which the atrial apertures of the zooids lead, while the oral apertures are towards their outer ends. In essential structure the zooids of such colonies (Fig. 682) resemble the simple Ascidians.

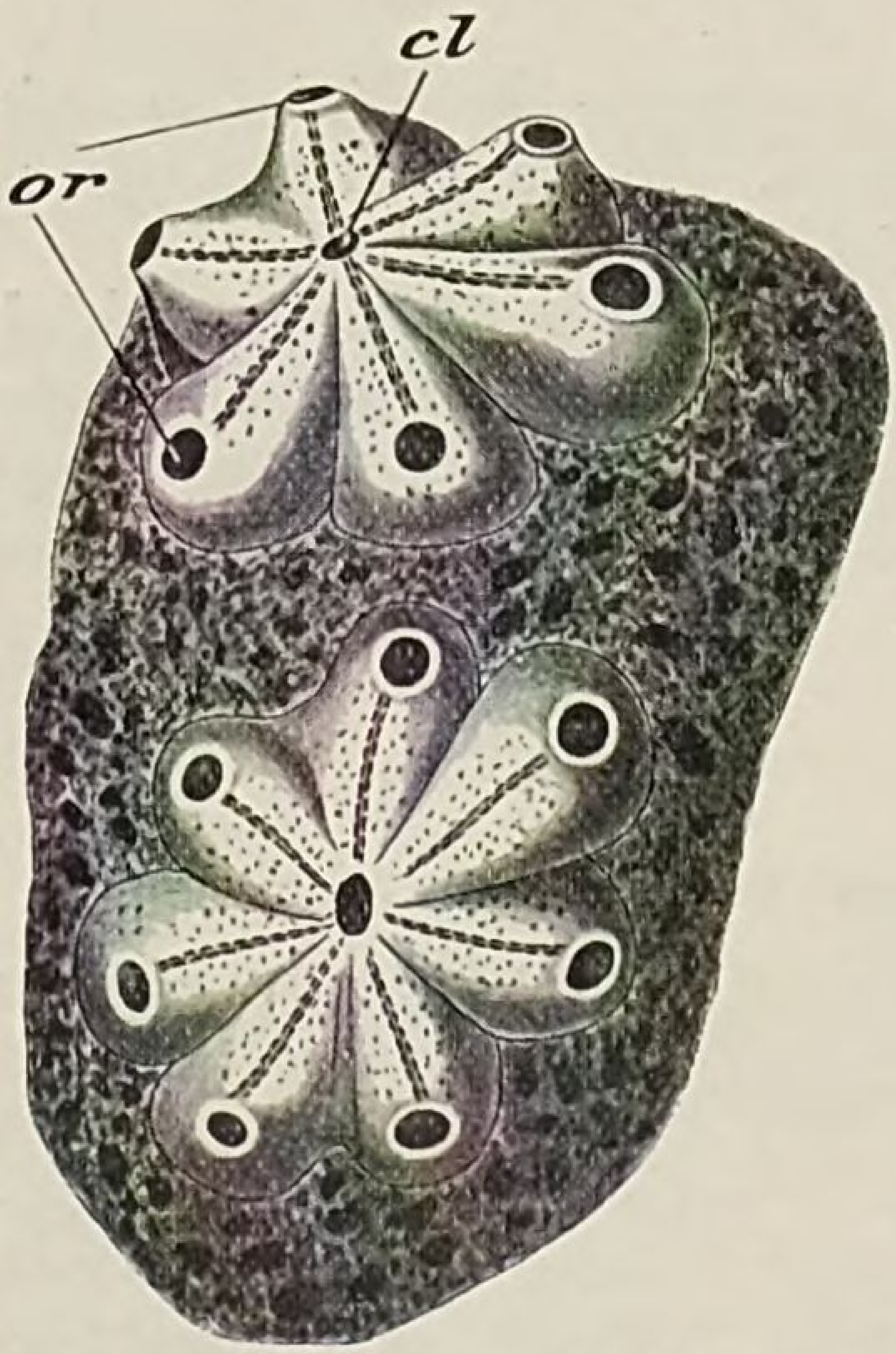


FIG. 681.—**Botryllus violaceus.** *or.* oral apertures; *cl.* opening of common cloacal chamber. (After Milne-Edwards.)

In the free-swimming pelagic *Doliolum* (Fig. 683) the shape is widely different from that of the ordinary fixed forms. The body is cask-shaped, surrounded as by hoops by a series of annular bands of muscular fibres (*mus. bds.*). The oral and atrial apertures (*or. ap.*, *atr. ap.*) instead of being situated near together at the same end of the body, are placed at opposite extremities, and the relations of the various organs have undergone a corresponding modification. The test is thin and transparent. Surrounding each opening is a series of lobes—the *oral* and *atrial lobes*—in which there are sense-organs; and the first and last of the

muscular hoops serve as sphincters for the two orifices. The oral aperture leads into a wide pharyngeal sac (*ph.*), occupying at least the anterior half of the body; its posterior wall alone is usually perforated by stigmata (*stig.*). An endostyle (*end.*) is present, and a peri-pharyngeal band; but there is no dorsal lamina. Doliolum moves through the water by the contractions of the muscular bands, which have the effect of driving the water backwards out of the branchial sac.

Salpa (Figs. 684–685) is nearly allied to Doliolum in its external features and internal structure. It has a fusiform body, usually somewhat compressed laterally, and with the oral and atrial cavities nearly terminal; but the muscular bands do not form complete hoops. The pharyngeal and atrial cavities take up the greater part of the space in the interior of the body, where they form an almost continuous cavity, being separated from one another only by an obliquely running vascular band, which represents the dorsal lamina of the fixed Ascidians, and is frequently termed the *branchia*.

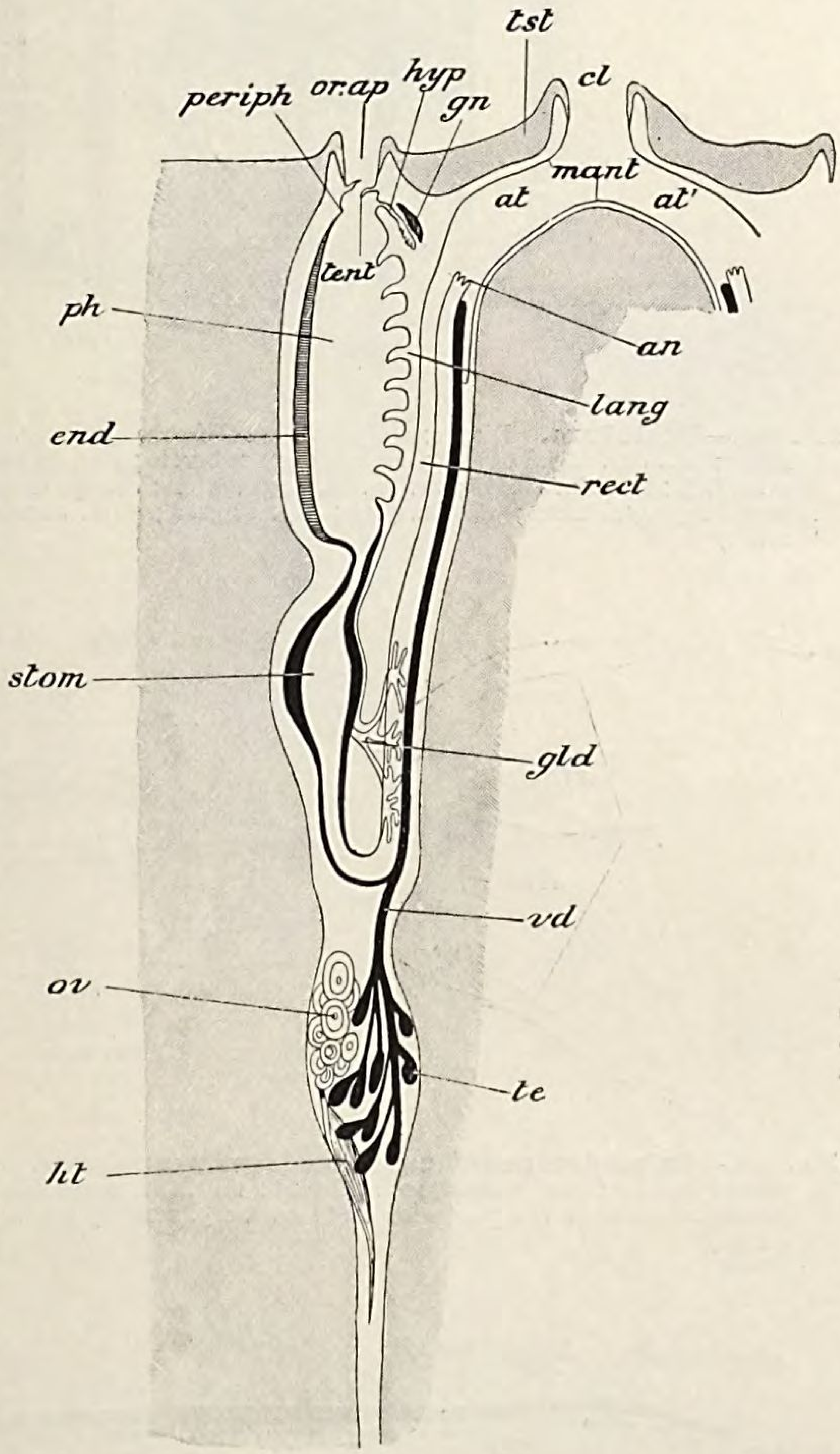


FIG. 682.—Diagram of a zooid of a colony of **Composite Ascidians,** in which the zooids are in pairs, as seen in a vertical section of the colony. *an.* anus; *at.* atrium; *at'.* atrium of adjoining zooid; *cl.* cloaca common to the two zooids; *end.* endostyle; *gld.* digestive gland; *gn.* nerve-ganglion; *ht.* heart; *hyp.* hypophysis; *lang.* languets; *mant.* mantle; *or. ap.* oral aperture; *ov.* ovary; *periph.* peri-pharyngeal band; *ph.* pharynx; *rect.* rectum; *stom.* stomach; *te.* testis; *tent.* tentacles; *tst.* test, or common gelatinous mass; *v. d.* vas deferens. (After Herdman.)

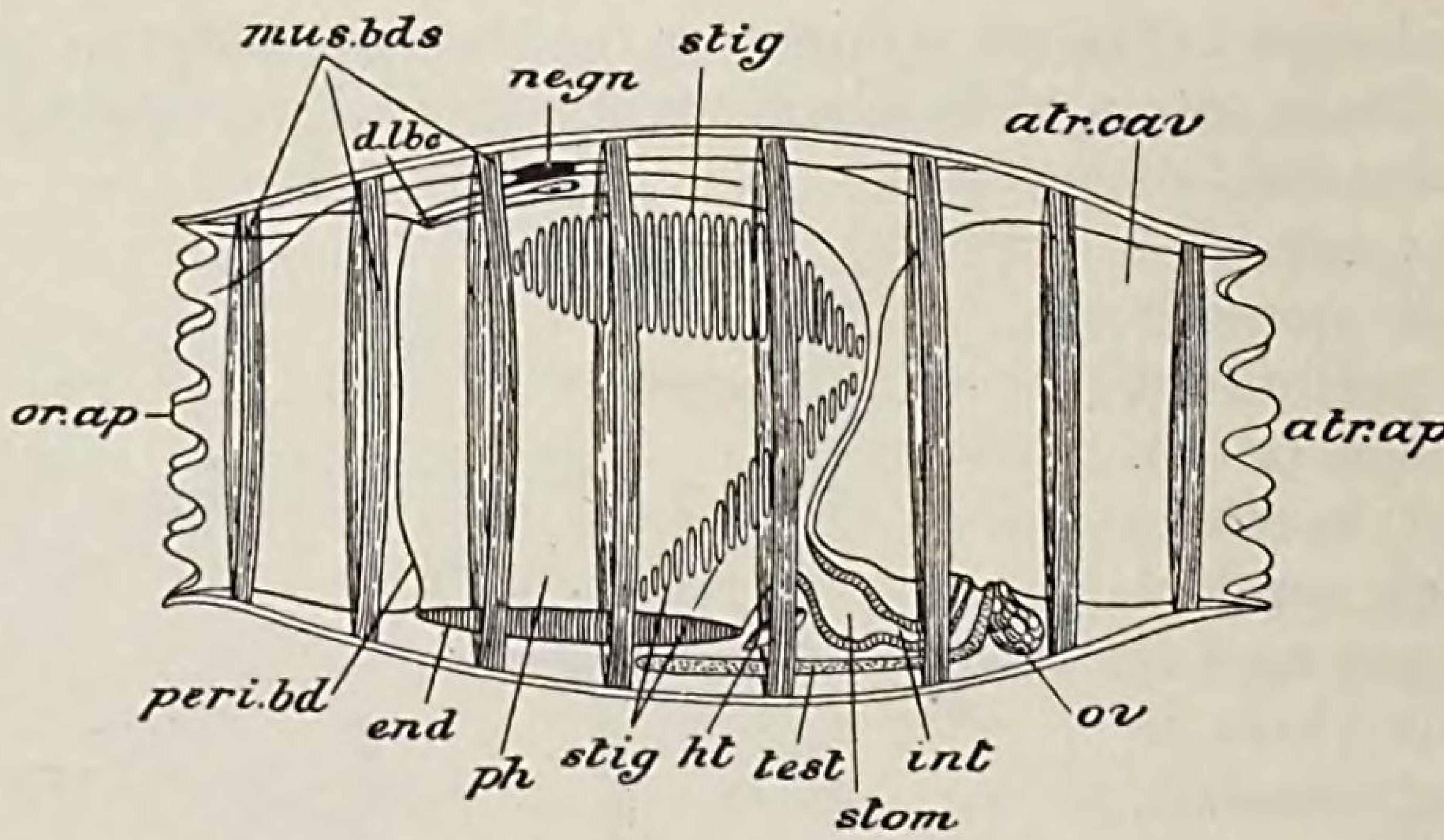


FIG. 683.—**Doliolum.** Diagram of the sexual form. *atr. ap.* atrial aperture surrounded by lobes; *atr. cav.* atrial cavity; *d. tbc.* dorsal tubercle; *end.* endostyle; *ht.* heart; *int.* intestine; *mus. bds.* muscular bands; *ne. gn.* nerve-ganglion; *or. ap.* oral aperture; *ov.* ovary; *peri. bd.* peripharyngeal band; *ph.* pharynx; *stig.* stigma; *stom.* stomach; *test.* testis. (After Herdman.)

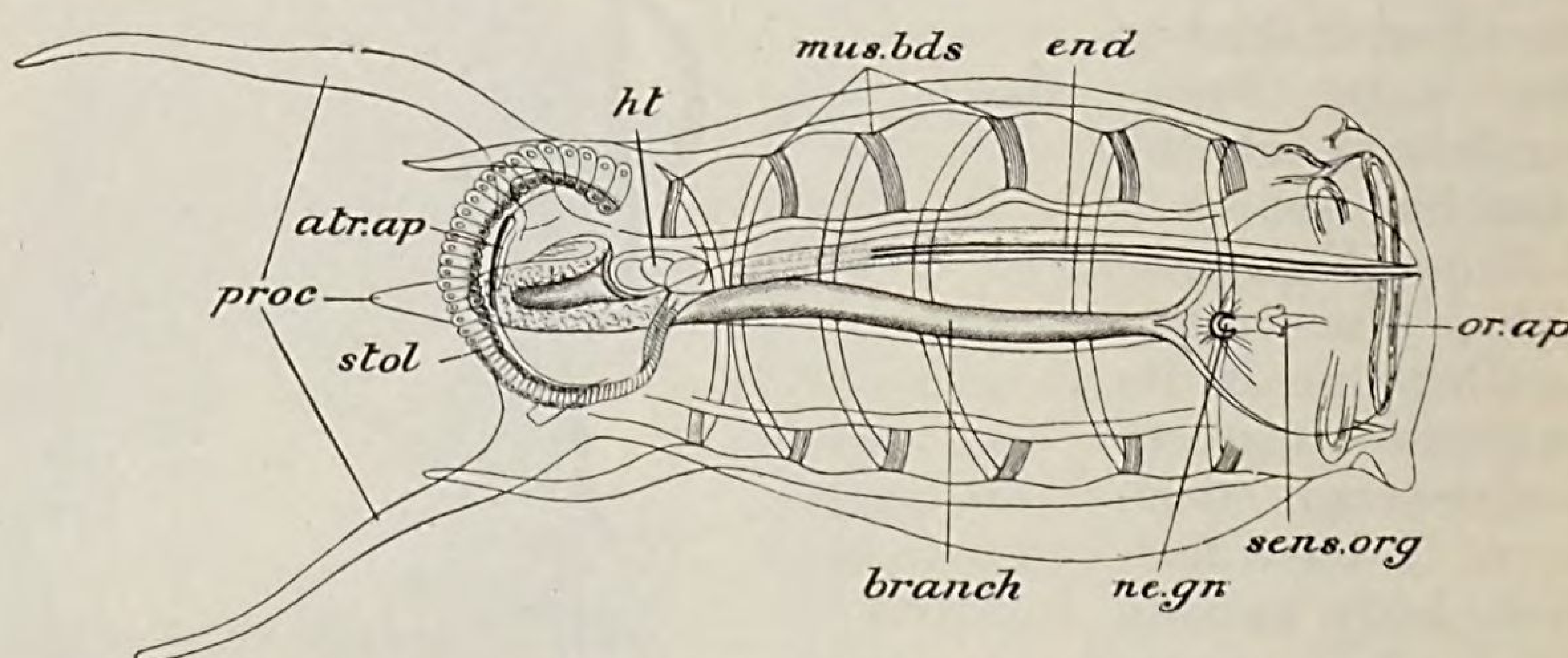


FIG. 684.—**Salpa democratica,** asexual form, ventral view. *atr. ap.* atrial aperture; *branch,* dorsal lamina; *end.* endostyle; *ht.* heart; *mus. bds.* muscular bands; *ne. gn.* nerve-ganglion; *proc.* processes at the posterior end; *sens. org.* sensory organ; *stol.* stolon. (After Vogt and Jung.)

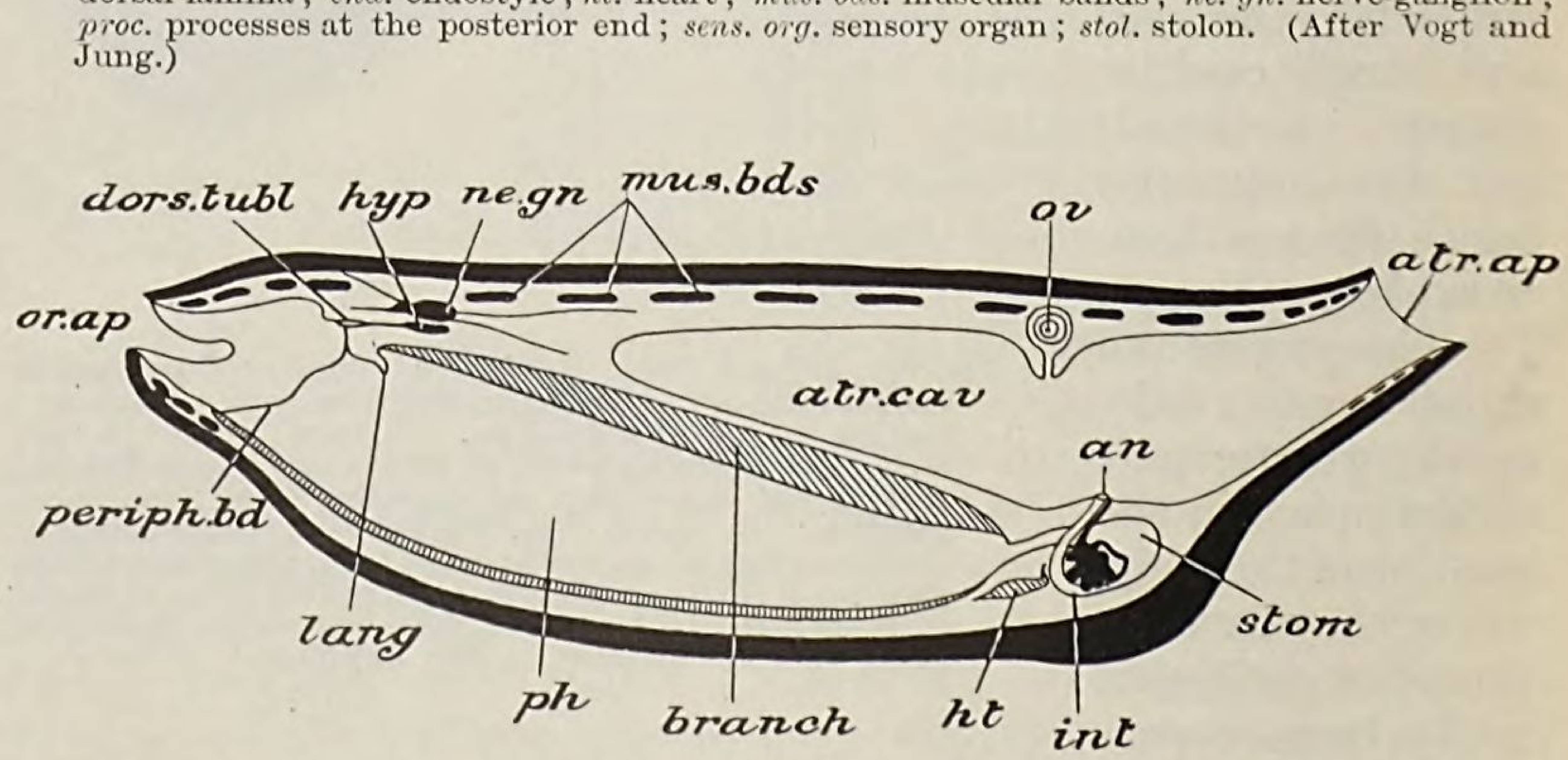


FIG. 685.—**Salpa,** semi-diagrammatic lateral view. *an.* anus; *atr. ap.* atrial aperture; *branch,* dorsal lamina; *dors. tubl.* dorsal tubercle; *ht.* heart; *hyp.* hypophysis; *lang.* languet; *mus. bds.* muscular bands; *ne.gn.* nerve ganglion; *or. ap.* oral aperture; *ov.* ovary in ovisac; *stom.* stomach (After Herdman.)

Octacnemus, allied to Salpa, appears to be fixed, and has the oral and atrial apertures towards one end of the body, which is somewhat discoid, with its margin produced into eight tapering processes.

Pyrosoma (Fig. 686) is a colonial Tunicate; the colonies of which are of a cylindrical form, with an orifice at one end and usually closed at the other. The oral apertures (Fig. 687, *or. ap.*) of the zooids are situated on the outer surface of the cylinder on the extremities of a series of papillæ. The colonies of Pyrosoma, which may be from two or three inches to four feet in length, are pelagic, and are brilliantly phosphorescent.

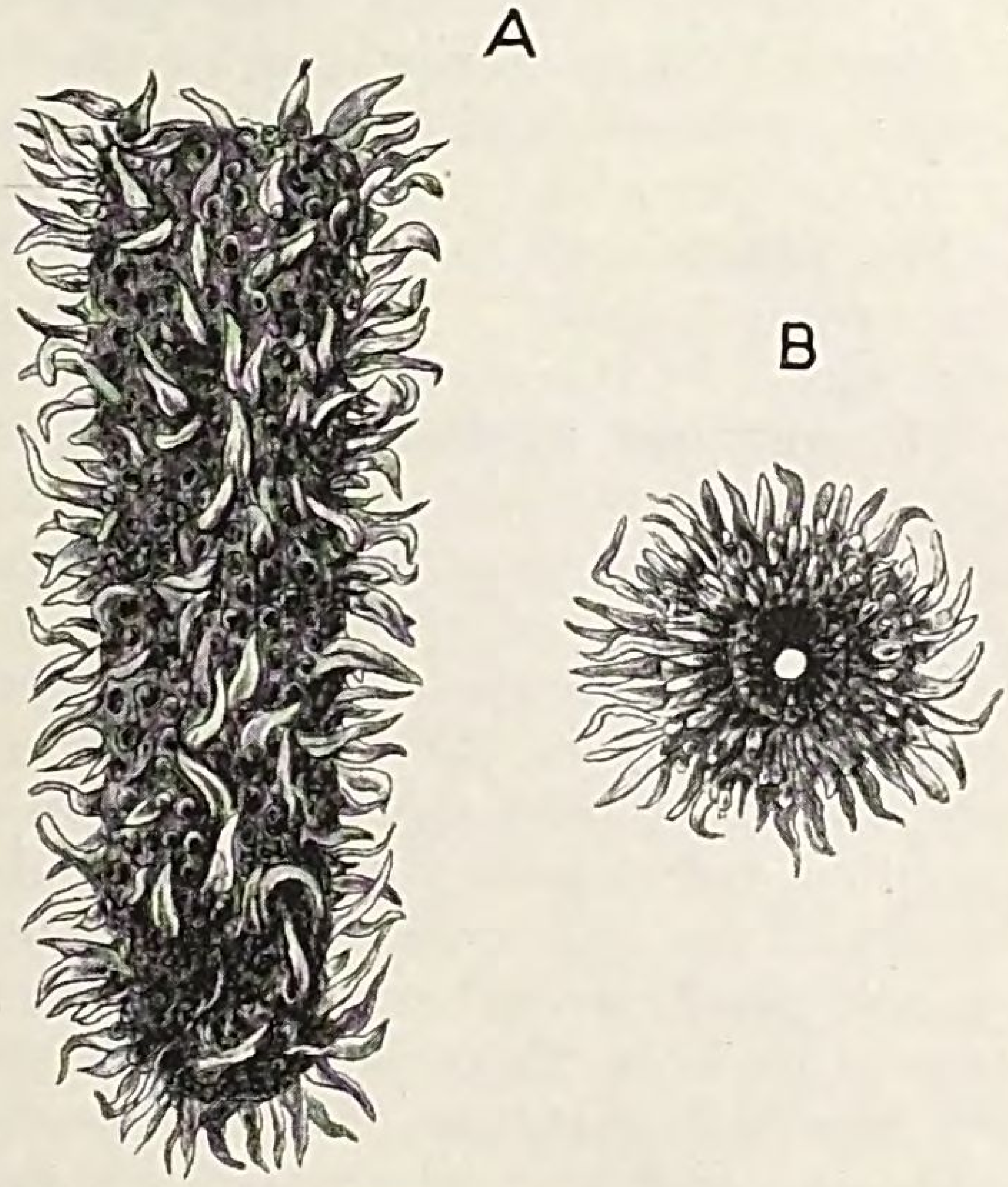


FIG. 686.—Colony of **Pyrosoma.** A, side view; B, end view. (After Herdman.)

The **enteric canal** in Appendicularia (Fig. 680) consists, in addition to the pharynx, of a narrow œsophagus, a bilobed stomach, and a straight intestine (*int.*) which opens directly by an anal aperture (*an.*) situated on the ventral side. In Oikopleura the intestine is absent. The alimentary canal of the simple Ascidians has already been described, and there are few differences of consequence in the various families; in the composite forms the arrangement of the parts is the same in all essential respects as in the simple.

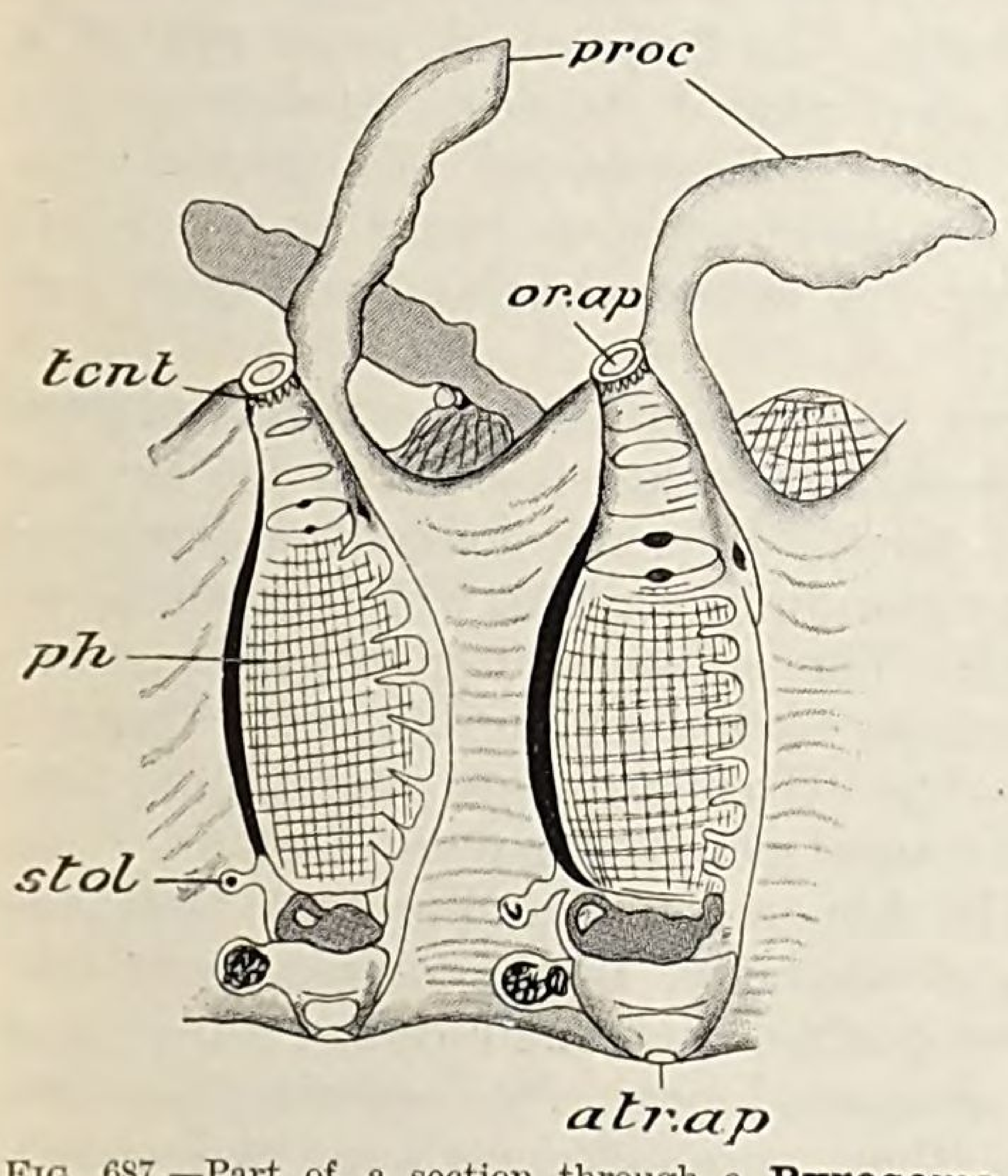


FIG. 687.—Part of a section through a **Pyrosoma** colony. *atr. ap.* atrial aperture; *or. ap.* oral aperture; *proc.* processes of test on outer surface of colony; *ph.* pharynx; *stol.* stolon on which are developed buds giving rise to new zooids; *tent.* tentacles. (After Herdman.)

In the Salpæ and in Doliolum and Octacnemus the alimentary canal forms a relatively small dark mass—the so-called *nucleus* —towards the posterior end of the body; it consists of œsophagus, stomach, and intestine, the anal aperture being situated in the peribranchial or atrial part of the internal cavity.

The **heart** in all has the simple structure already described in the simple Ascidian. In Appendicularia its wall consists of only two cells. In Oikopleura it is apparently absent.

The **nervous system** in Appendicularia consists of a *cerebral ganglion* (Fig. 680, *ne. gn.*) at the side of the mouth on the dorsal side, of a dorsal nerve which passes from this to a *caudal ganglion* (*ne. gn'.*) at the root of the tail, and of a caudal nerve (*ne'.*) which passes from this to the extremity of the tail, presenting at intervals slight enlargements from which nerves are given off. An otocyst (*oto.*) and a pigment-spot are placed in close relation to the cerebral ganglion, and close to it also is a tubular process opening into the branchial sac and evidently representing the duct of the sub-neural gland of the simple Ascidian. In the simple Ascidians, as we have seen, there is a single flattened ganglion, representing the cerebral ganglion of Appendicularia, situated between the oral and atrial apertures; and the same holds good of the composite forms. Many of the simple Ascidians have pigment-spots, probably of a sensory character, around the oral and atrial apertures. In Salpa and Doliolum there is also a single ganglion (Figs. 683, 684 and 685, *ne. gn.*) situated dorsally, giving off nerves to the various parts of the body. In Salpa there is an eye of a simple character and an otocyst placed in close relation to the ganglion in addition to eye-like bodies devoid of pigment: in Doliolum these are absent, but pigment spots occur in the lobes surrounding the oral opening. A subneural gland and duct are present in both these genera.

In the simple Ascidian we have seen that the **renal organ** consists of a number of large clear vesicles situated in the loop of the intestine and devoid of duct. In some forms the terminal portion of the spermiduct has glandular walls in which concretions of uric acid have been found. The sub-neural gland is by some zoologists looked upon as perhaps having an excretory function.

Reproductive system.—The Urochorda are hermaphrodite. Ovary and testis are in all cases simple organs placed in close relation with one another. In Appendicularia (Fig. 680) they are situated in the aboral region of the body. In the simple Ascidians, they may be either single or double, and their ducts, sometimes very short, sometimes more elongated, open close together into the atrial cavity. In Pyrosoma there are no gonoducts, the ovary, which contains only a single ovum, and the testis being lodged in a diverticulum of the peribranchial cavity. In Salpa also the ovary contains usually only a single ovum: ovary and testis lie in

close relation to the alimentary canal in the "nucleus," and their short ducts open into the peribranchial cavity. In Doliolum the elongated testis and oval ovary have a similar position to that which they occupy in Salpa, but the ovary consists of a number of ova.

Development and Metamorphosis.—Usually impregnation takes place after the ova have passed out from the atrial cavity. But in a few simple and many compound forms impregnation takes place in the atrium, and the ovum remains there until the tailed larval stage is attained. In certain composite forms there is a coalescence of the embryo with the wall of the atrium, forming a structure analogous to the *placenta* of the Mammals and designated by that term. Self-impregnation is usually rendered impossible by ova and sperms becoming mature at different times; but sometimes both become ripe simultaneously, and self-impregnation is then possible.

A somewhat complicated series of membranes invests the ovum. The immature ovarian ovum is enclosed in a layer of flat cells—the primitive *follicle cells*—derived from indifferent cells of the ovary. On the surface of this is developed a structureless basal membrane. The follicle cells increase by division and soon form a sphere of cubical cells. Certain of the cells migrate into the interior of the sphere so as to form a layer on the surface of the ovum. Others penetrate into the latter so as to lie in the superficial strata of the yolk. The layer of cells on the surface of the ovum are termed the *testa cells:* they afterwards develop on the outer surface a thin structureless layer, the *chorion.* Meantime, external to the follicle cells, between them and the basal membrane, has appeared a layer of flattened epithelial cells; this, with the basal membrane, is lost before the egg is discharged. In all the simple Ascidians, with the exception of the few in which development takes place internally, the protoplasm of the follicle cells becomes greatly vacuolated, so as to appear frothy, and the cells become greatly enlarged, projecting like papillæ on the surface and buoying up the developing ovum.

Segmentation is complete and approximately equal, but in the eight-cell stage four of the cells are smaller and four larger. The smaller, situated on the future ventral side, are the beginnings of the ectoderm; the four larger form the endoderm, but also perhaps give origin to a number of small ectoderm cells. A small segmentation-cavity (Fig. 688, *A*, *seg. cav.*) appears early. A curvature of the embryo then supervenes, so that the side on which the larger cells are situated becomes concave, and the larger cells thus become invaginated within the smaller, obliterating the segmentation cavity, the result being the formation of a gastrula stage (*B*) with an archenteron. The blastopore, at first very wide, gradually becomes narrowed to a comparatively small rounded aperture (*C*)

which at the same time changes its position until it becomes placed at what is destined to be the posterior end of the dorsal surface.

The embryo elongates in the direction of the future long axis. The dorsal surface becomes recognisable by being flatter, while the ventral remains convex. The ectoderm cells bordering the blastopore become distinguished from the rest by their more cubical

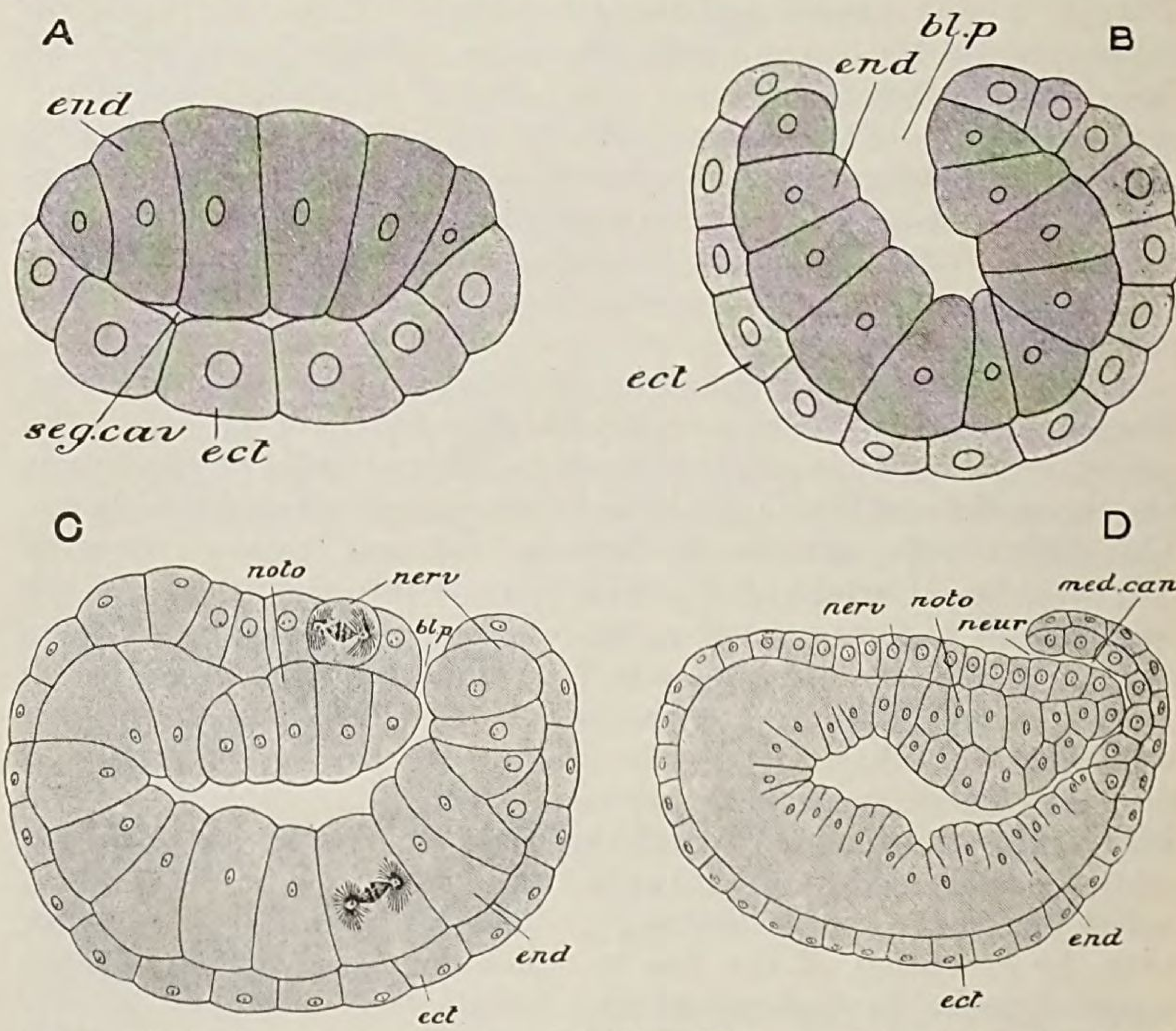


FIG. 688.—Early stages in the development of **Clavellina.** *A*, flattened blastula; *B*, early gastrula; *C*, approximately median optical section of more advanced gastrula in which the blastopore has become greatly reduced and in which the first rudiment of the notochord is discernible; *D*, similar view of a later larva in which the medullary canal has begun to be closed in posteriorly. *bl. p.* blastopore; *ect.* ectoderm; *end.* endoderm; *med. can.* medullary canal; *nerv.* cells destined to give rise to the nerve-cord; *neur.* neuropore; *noto.* notochord; *seg. cav.* segmentation cavity. (*A* and *B* from Korschelt and Heider after Seeliger, *C* and *D* after Van Beneden and Julin.)

shape; these cells, which form the earliest rudiment of the nervous system, become arranged in the form of a plate—the *medullary plate*—on the dorsal surface. On the surface of this plate appears a groove—the medullary groove—bounded by right and left *medullary folds*, which pass into one another behind the blastopore. At the same time a number of small cells of the inner layer in the neighbourhood of the blastopore form a ring round that opening, and then extend forwards in the form of a plate below the medullary plate. The middle portion of this subsequently forms

the rudiment of the posterior portion of the notochord; the lateral parts go to form the caudal part of the mesoderm.

The medullary folds grow upwards and inwards over the medullary groove, and unite together (*D*), the union beginning behind and progressing forwards, in such a way as to form a canal, the *neurocœle*, in the hinder portion of which is the opening of the blastopore. In this process of closing-in of the medullary groove the fold which passes round behind the blastopore takes an important part, growing forwards over the posterior part of the canal. The blastopore thus enclosed in the medullary canal persists for a time as a small opening—the *neurenteric canal*—by which the neurocœle and enteric cavity are placed in communication. At the anterior end of the medullary canal, owing to its incomplete closure in this region, there remains for a time an opening—the *neuropore* (Fig. 689, *neur.*)—leading to the exterior.

The embryo (Fig. 689, *B*) now becomes pear-shaped, the narrow part being the rudiment of the future tail. As this narrow part elongates the part of the enteric cavity which it contains soon disappears, coming to be represented only by a cord of endoderm cells. In the anterior wide part of the embryo the mesoderm (*mes.*) arises by the formation of paired outgrowths, which arise from the dorsal wall of the archenteron. A row of endoderm cells between the two sets of outgrowths represent the rudiments of the trunk part of the notochord; they become arranged to form a cylindrical cord.

The caudal region increases in length rapidly, and the anterior or trunk region, at first round, becomes oval. At its anterior end there appear three processes of the ectoderm, the rudiments of the *adhesive papillæ* (Fig. 690, *adh.*), organs by which the larva subsequently becomes fixed. The ectoderm cells at an early stage secrete the rudiments of the cellulose test; in the caudal region this forms longitudinal dorsal and ventral flaps having the function of unpaired fins.

The medullary canal becomes enlarged at its anterior end. A vesicular outgrowth from this enlarged anterior portion forms the *sense-vesicle* (*sens. ves.*). The posterior narrow part forms the caudal portion of the central nervous system (spinal cord). Masses of pigment in relation to the sense-vesicle early form the rudiment of the two larval sense-organs, otocyst and eye. The part behind this presents a thickened wall with a narrow lumen. This is known as the *ganglion of the trunk*. The rudiment of the hypophysis early appears as a ciliated diverticulum (*cil. gr.*) of the anterior end of the archenteron.

The embryonic alimentary canal consists of two regions, a wide region situated altogether in front of the notochord, and a narrower portion situated behind in the region of the notochord. The wider anterior part gives rise to the pharynx; the posterior part

to the œsophagus, stomach, and intestine. The mouth-opening is formed shortly before the escape of the embryo from the egg; an

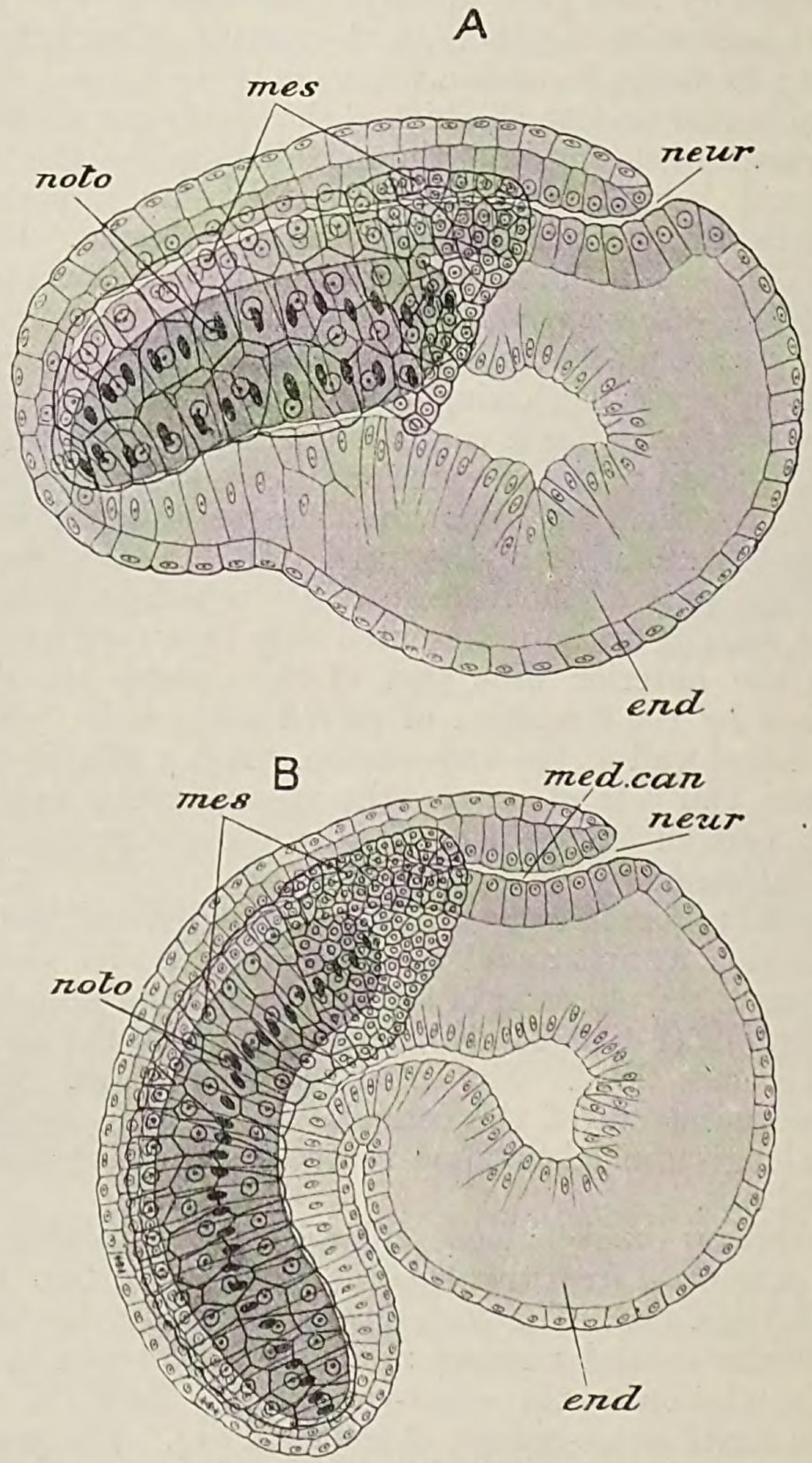


FIG. 689.—Later stages in the development of **Clavellina.** *A*, approximately median optical section of a larva in which the medullary canal (neurocœle) has become enclosed throughout, communicating with the exterior only by the neuropore at the anterior end, and with the archenteron by the neurenteric canal; *B*, larva with a distinct rudiment of the tail and well-formed mesoderm layer and notochord. Letters as in preceding figure; in addition, *mes*. mesoderm. (After Van Beneden and Julin.)

ectodermal invagination is formed at the anterior end, and an endodermal diverticulum from the archenteron grows out to meet it; the two coalesce, and the oral passage is thus formed.

The first beginnings of the atrial cavity appear about the same time as a pair of invaginations of the ectoderm which grow inwards and form a pair of pouches, each opening on the exterior by an opening. There is some difference of opinion as to some points in the history of these atrial pouches. According to one account each gives off a diverticulum inwards towards the pharynx, while from the latter a pair of diverticula grow outwards to meet them; the two sets of diverticula subsequently meet and unite to form a pair of passages, one leading from each atrial pouch to the pharynx; these form the first pair of stigmata. The atrial pouches then extend round the pharynx until they form a narrow space completely surrounding it, the cavities of the two pouches coalescing, and a number of perforations of the pharynx placing its cavity in direct communication with the surrounding space. According to another account two endodermal diverticula from the primitive pharynx grow out and open into the atrial pouches; these diverticula subsequently become greatly expanded and grow round the pharynx to form the peri-pharyngeal space. It will be observed that, while according to the former of these two views the peri-pharyngeal space is ectodermal in origin, according to the latter it is endodermal. The two openings of the atrial pouches subsequently coalesce to form one—the permanent atrial aperture.

It will be useful now, at the cost of a little repetition, to summarise the various characteristics of the larval Ascidian at the

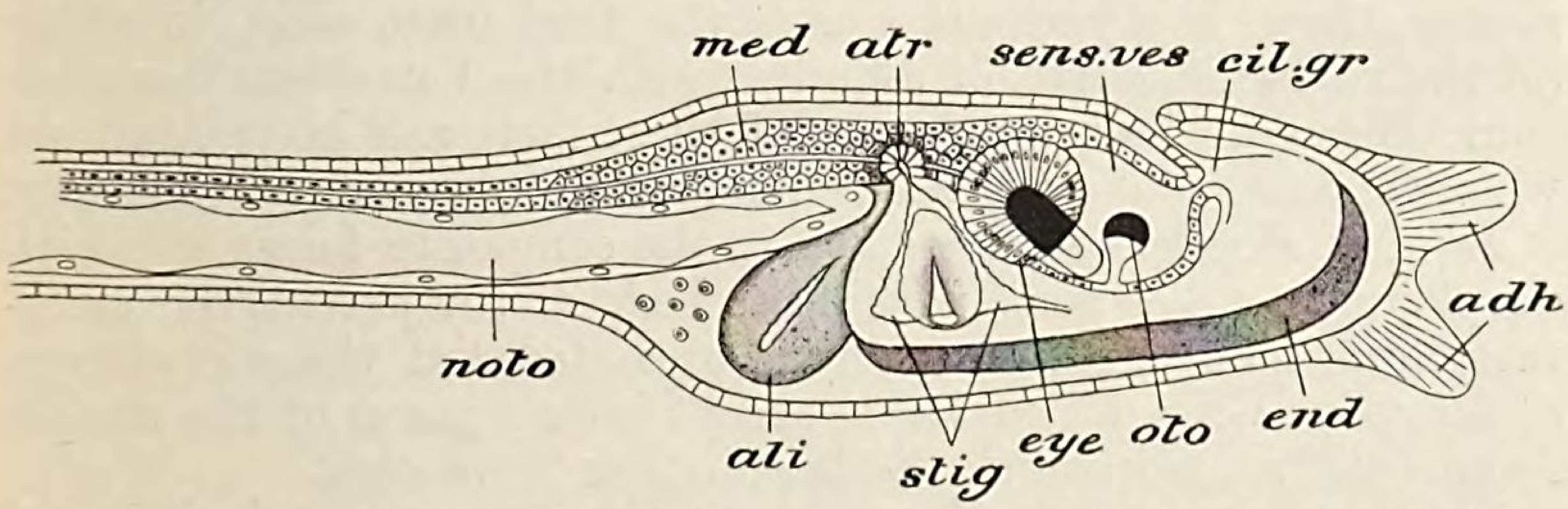


FIG. 690.—Free-swimming larva of **Ascidia mammillata,** lateral view. *adh.* adhesive papillæ; *ali.* alimentary canal; *atr.* atrial aperture; *cil. gr.* ciliated groove; *end.* endostyle; *eye*, eye; *med.* nerve cord; *noto.* notochord; *oto.* otocyst; *sens. ves.* sense-vesicle; *stig.* earliest stigmata. (From Korschelt and Heider, after Kowalewsky.)

stage when it escapes from the egg and becomes free-swimming (Fig. 690). In general shape it bears some resemblance to a minute tadpole, consisting of an oval trunk and a long, laterally-compressed tail. The tail is fringed with a caudal fin, which is merely a delicate outgrowth of the thin test covering the whole of the surface; running through the delicate fringe are a series of striæ, presenting somewhat the appearance of the fin-rays of a Fish's fin. In the axis of the tail is the notochord (*noto.*), which at this stage consists of a cylindrical cord of gelatinous substance

enclosed in a layer of cells. Parallel with this runs, on the dorsal side, the narrow caudal portion of the nerve-cord, and at the sides are bands of muscular-fibres. In the trunk the nerve-cord is dilated to form the ganglion of the trunk, and, further forwards, expands into the sense-vesicle (*sens. ves.*) with the otocyst (*oto.*) and eye (*eye*). The enteric canal is distinguishable into pharynx, œsophagus, stomach and intestine. The pharynx opens on the exterior by the mouth: in its ventral floor the endostyle (*end.*) has become developed; its walls are pierced by stigmata, the number of which varies; a ciliated sac (*cil. gr.*) opens into it below the trunk part of the nerve-cord. The atrial cavity has grown round the pharynx, and opens on the exterior by a single aperture only (*atr.*). The heart and pericardial cavity have become developed. In this tailed free-swimming stage the larva remains only a few hours; it soon becomes fixed by the adhesive papillæ, and begins to undergo the *retrogressive metamorphosis* by which it attains the adult condition.

The chief changes involved in the retrogressive metamorphosis (Fig. 691) are the increase in the number of pharyngeal stigmata, the diminution, and eventually the complete disappearance, of the tail with the contained notochord and caudal part of the nerve-cord, the disappearance of the eye and the otocyst, the dwindling of the trunk part of the nervous system to a single ganglion, and the formation of the reproductive organs. Thus, from an active, free-swimming larva, with well-developed organs of special sense, and provided with a notochord and well-developed nervous system, there is a retrogression to the fixed inert adult, in which all the parts indicative of affinities with the Vertebrata have become aborted. The significance of these facts will be pointed out when we come to discuss the general relationships of the Chordata.

In some simple Ascidians, and in the composite forms in which development takes place within the body of the parent, the metamorphosis may be considerably abbreviated, but there is always, so far as known, a tailed larva, except in one genus of the simple forms (*Molgula*), in which the tailed stage is wanting.

In Pyrosoma development is direct, without a tailed larval stage, and takes place within the body of the parent. The ovum contains a relatively large quantity of food-yolk, and the segmentation is meroblastic. A process, developed at an early stage, elongates to form the so-called *stolon*, which divides, by the formation of constrictions, into four parts, each destined to give rise to a zooid; and this group of *tetrazooids*, as they are termed, gives rise by budding to an entire colony.

The development of Doliolum is, in all essential respects, very like that of the simple Ascidians. There is total segmentation, followed by the formation of an embolic gastrula; the larva (Fig. 692) has a tail with a notochord (*noto.*), and a body in which the characteristic muscular bands soon make their appearance. By

and by the tail aborts, and two processes, one postero-dorsal, the other ventral, known respectively as the *dorsal* (*dors. st.*) and *ventral*

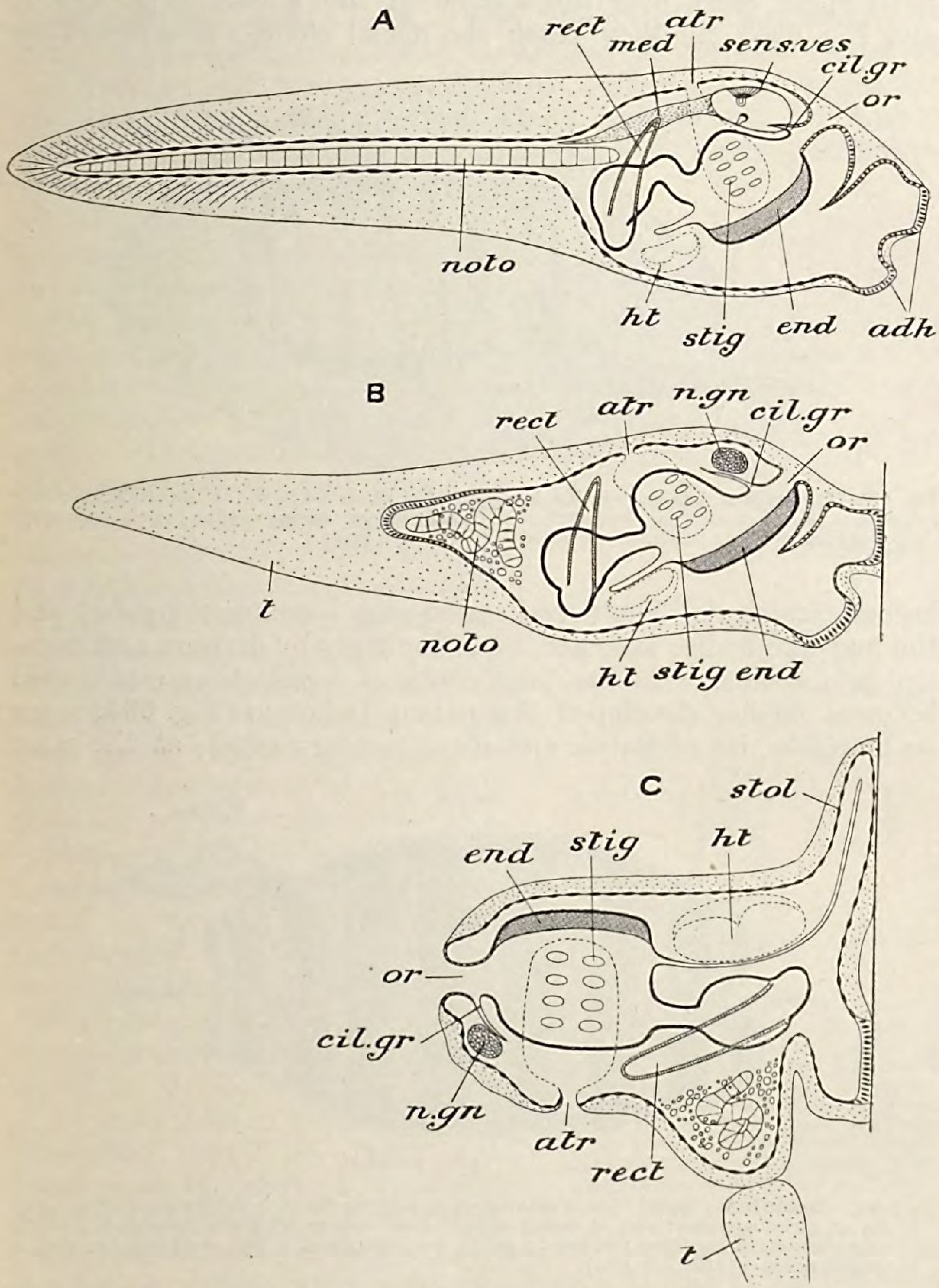


FIG. 691.—Diagram of the metamorphosis of the freetailed larva into the fixed Ascidian. *A*, stage of free-swimming larva; *B*, larva recently fixed; *C*, older fixed stage. *adh.* adhesive papillæ; *atr.* atrial cavity; *cil. gr.* ciliated groove; *end.* endostyle; *ht.* heart; *med.* ganglion of trunk; *n. gn.* nerve-ganglion; *noto.* notochord; *or.* oral aperture; *rect.* rectum; *sens. ves.* sense vesicle; *stig.* stigmata; *stol.* stolon; *t.* tail. (From Korschelt and Heider, after Seeliger.)

stolons (*vent. st.*), grow out from the body of the larva. On the latter are formed a number of slight projections or buds. These

become constricted off, and in the form of little groups of cells, each consisting of seven strings of cells with an ectodermal investment, creep over the surface of the parent (Fig. 693, *e*, and Fig. 694) till they reach the dorsal stolon, to which they

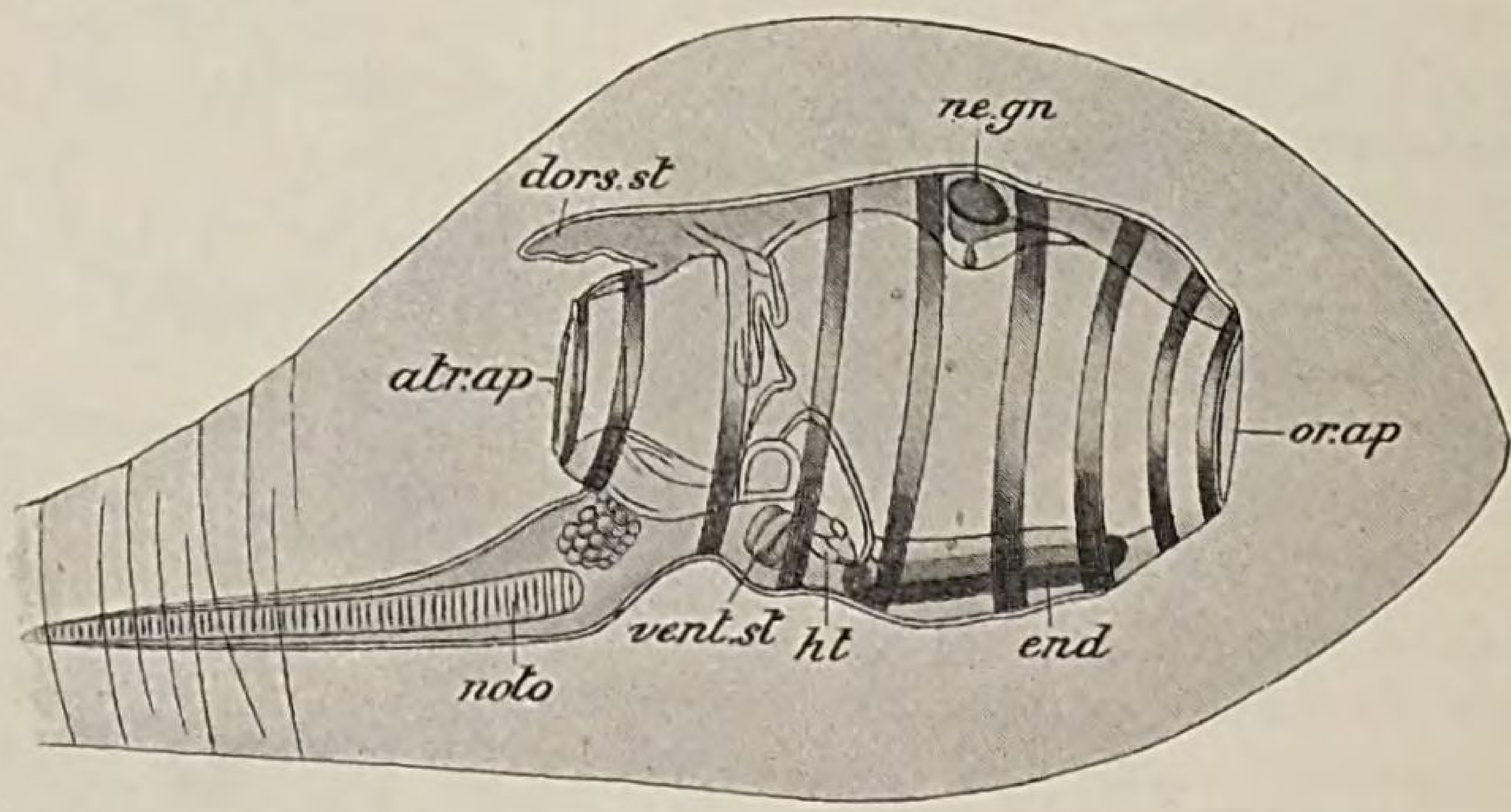


FIG. 692.—**Doliolum,** late stage in the development of the tailed larva. *atr. ap.* atrial aperture; *dors. st.* dorsal stolon; *end.* endostyle; *ht.* heart; *ne. gn.* nerve-ganglion; *noto.* notochord; *or. ap.* oral aperture; *vent. st.* ventral stolon. (After Uljanin.)

become attached. The dorsal stolon soon becomes elongated, and the bud-like bodies attached to it multiply by division and develop into zooids. As the long chain of zooids thus established becomes farther developed, the parent Doliolum (Fig. 694) loses its branchiæ, its endostyle and its alimentary canal; at the same

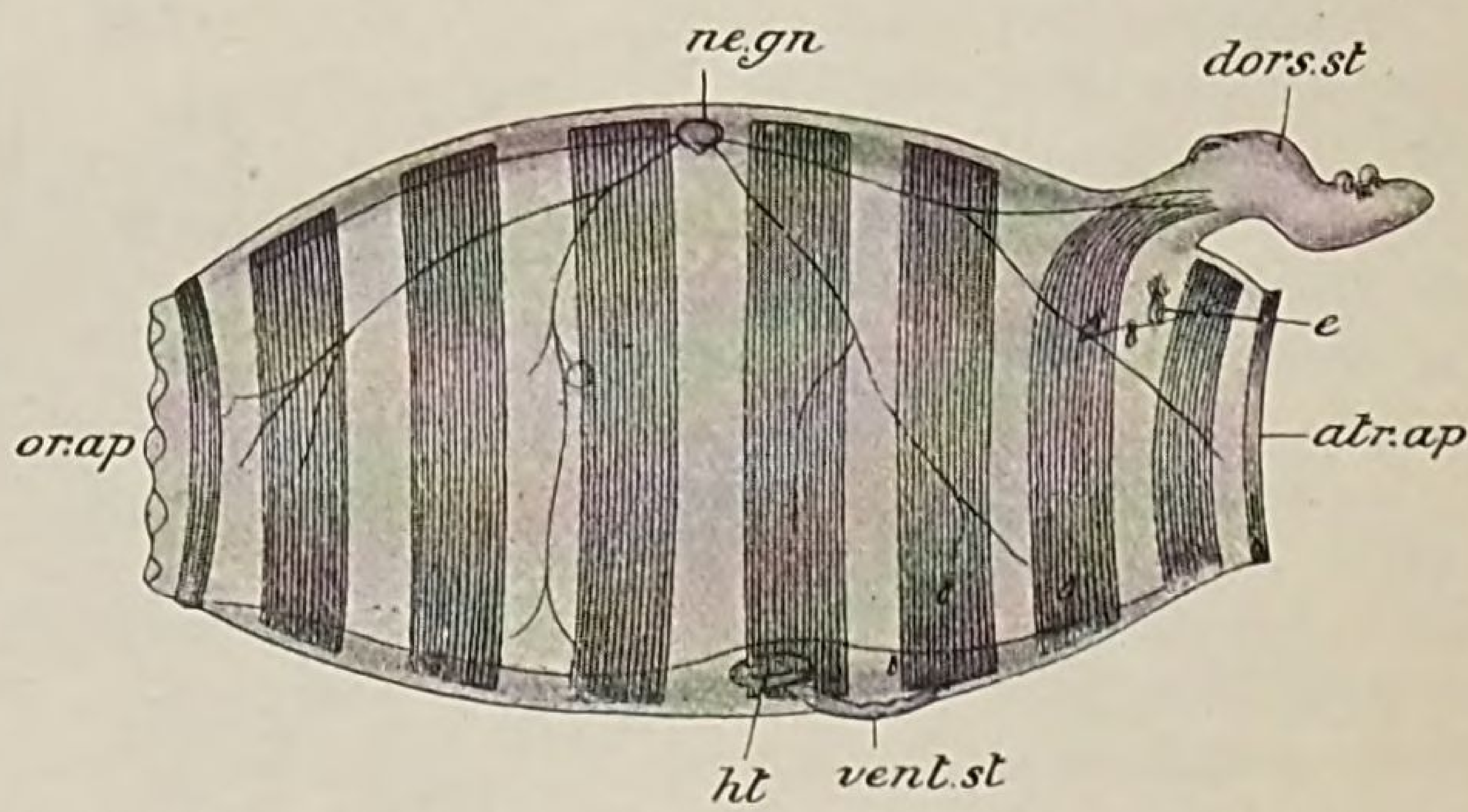


FIG. 693.—**Doliolum,** lateral view of asexual stage, showing the early development of the buds. *atr. ap.* atrial aperture; *dors. st.* dorsal stolon; *e.* embryos passing over the surface from the ventral stolon to the dorsal; *ht.* heart; *ne. gn.* nerve-ganglion; *or. ap.* oral aperture; *vent. st.* ventral stolon. (After Uljanin.)

time the muscle-bands increase in thickness, and the nervous system attains a higher development, until the whole parent comes to resemble, in a certain sense, the nectocalyx of a Siphonophore (Vol. I. p. 147), its exclusive function being by its contractions to propel the colony through the water.

The zooids of the dorsal stolon consist of two sets, differing from one another in position and in future history—the *lateral zooids* and the *median zooids.* The lateral zooids serve solely to carry on the nourishment and respiration of the colony, and do not undergo any further development. The median zooids, on the other hand, become detached, and each develops a ventral stolon. On this are found buds which have either migrated with the rest from the ventral stolon of the parent or have become developed in sitû. Each of these buds develops into a sexual Doliolum.

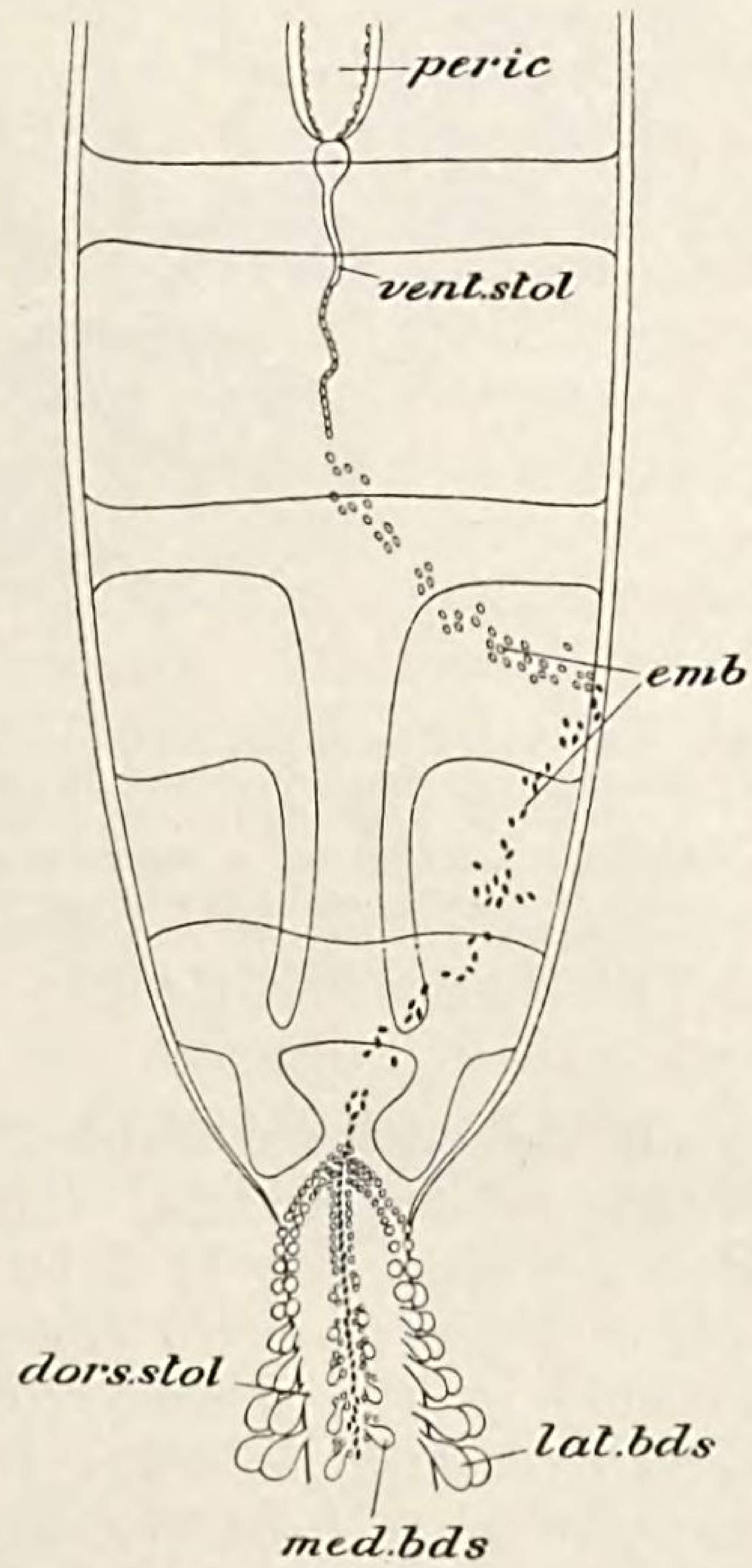


FIG. 694.—**Doliolum,** dorsal view of the posterior part of the body of an asexual zooid showing the course taken by the buds (*emb.*) over the surface from the ventral stolon (*vent. stol.*) to the dorsal (*dors. stol.*) and their growth on the latter. *lat. bds.* lateral buds; *med. bds.* median buds; *peric.* pericardium. (After Barrois)

The succession of stages in the life-history of Doliolum thus briefly sketched will be seen to succeed one another in the following order:—(1) sexual form; (2) tailed larva developed sexually from (1); (3) first asexual form the direct outcome of (2); (4) second asexual form developed on the dorsal stolon of (3) from buds originating on the ventral stolon; (5) the young of the sexual form (1) which are developed on the stolon of 4 from buds which were either formed there, or derived originally from the ventral stolon of 3.

Salpa, like Doliolum, presents a remarkable alternation of generations. In the sexual form, which has already been described, only one ovum becomes developed. The testis becomes mature later than the ovum, and the latter is impregnated by sperms from the testis of an individual of an older chain. The development is direct and takes place within the body of the parent, the embryo as it grows projecting into the branchial cavity. The nourishment of the developing embryo (Fig. 695) is effected by the formation of a structure—the *placenta*—through which a close union is brought about between the vascular system of the parent and that of the embryo. The placenta of Salpa is partly formed from follicle-cells and ectoderm cells of the embryo, partly from the cells of the wall of the oviduct. Segmentation is complete. The study of the earlier stages is complicated by the very remarkable and unusual circum-

stance that during segmentation there is a migration inwards of some of the cells of the follicle and of the wall of the oviduct, which enter the segmenting ovum and pass among the blastomeres. There is uncertainty as to what part these inwardly-migrating cells play in the development of the embryo. According to one observer they act merely as carriers of nourishment, and become broken up and eventually completely absorbed; according to another they actually displace the blastomeres and give rise to the greater part of the embryo.

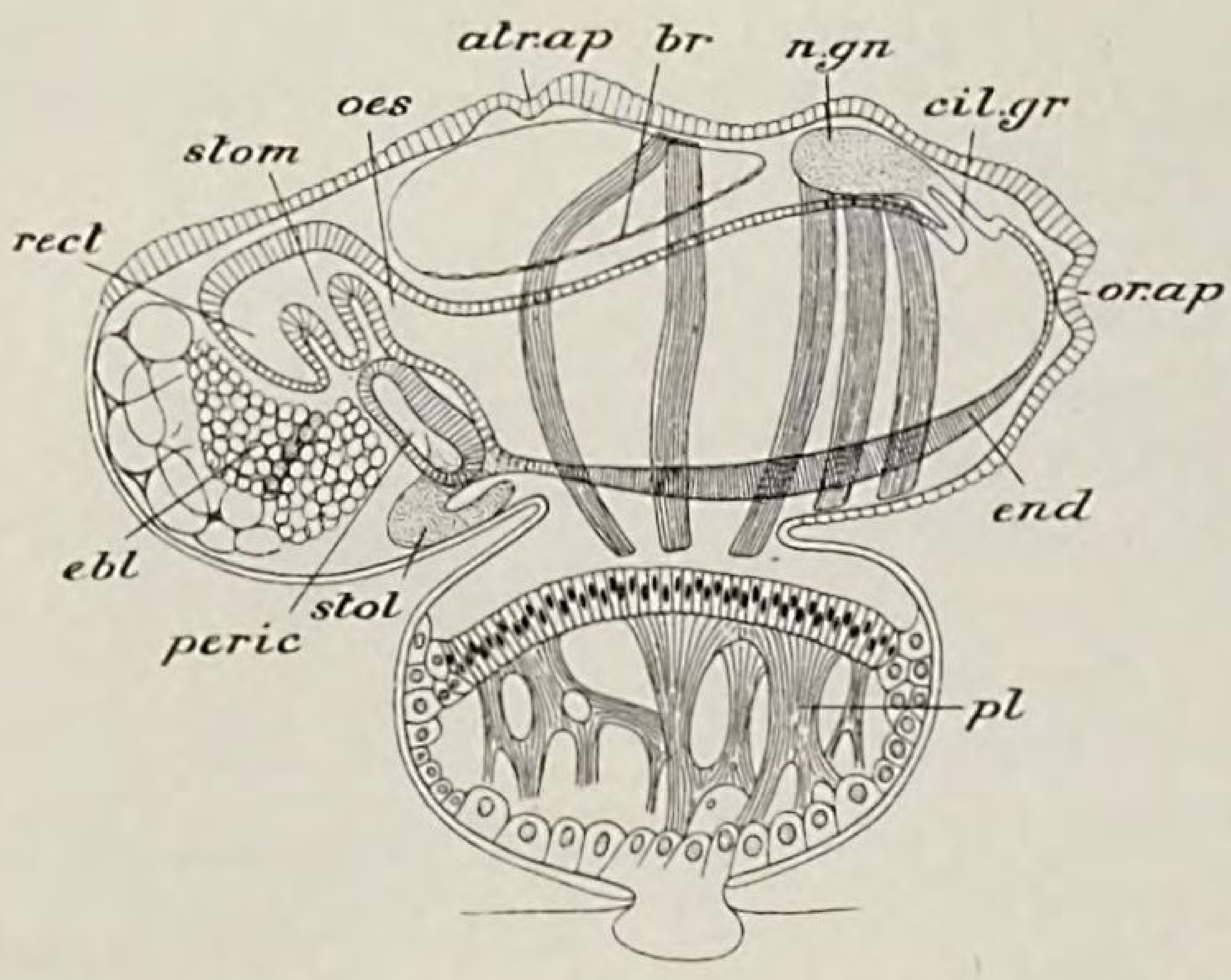


FIG. 695.—Late stage in the development of **Salpa,** showing the placental connection with the parent. *atr. ap.* atrial aperture; *br.* branchia; *cil. gr.* ciliated groove; *ebl.* elæoblast; *end.* endostyle; *n. gn.* nerve-ganglion; *œs.* œsophagus; *or. ap.* oral aperture; *peric.* pericardium; *pl.* placenta; *rect.* rectum; *stol.* stolon; *stom.* stomach. (From Korschelt and Heider, after Salensky.)

There is no tailed larval stage, and the embryo develops the muscle-bands and all the characteristic parts of the adult while still enclosed within the body of the parent and nourished by means of the placenta. This sexually-developed embryo, however, does not give rise to a form exactly like the parent, but to one which differs from the latter in certain less important features and notably in the absence of reproductive organs. The sexually formed embryo, in other words, forms an asexual generation. It escapes to the exterior and becomes free-swimming (Fig. 684). After a time there is developed a process or stolon (*stol.*), on the surface of which are formed a number of bud-like projections. These increase in size as the stolon elongates and each eventually assumes the form of a sexual Salpa. The stolon with the Salpæ attached becomes separated off and swims about as a chain of zooids in which the reproductive organs become developed.

Distribution, etc.—The pelagic forms are, as is the case with most pelagic organisms, of very wide distribution, and none of the genera are confined to particular oceanic areas. The fixed forms, both simple and composite, are also of world-wide distribution; they are much more abundant in the southern hemisphere than in the northern—the composite forms attaining their maximum in the South Pacific area. The depth to which the pelagic forms extend has not been determined. Fixed forms occur at all depths, but are much more numerous in shallow water than in deep, and

at great depths are comparatively poorly represented, the simple forms extending to a greater depth than the composite. Several genera of pedunculated simple forms seem to be confined to very great depths.

Though placed so high in the animal series, the Urochorda exhibit very low functional development. This is chiefly connected with the sessile condition of most of them. The movements performed by an Ascidian are slow and very limited in character, being confined to contractions of the mantle; when the animal is detached such contractions may be sometimes observed to result in a slow creeping locomotion. Even in the free forms the movements are limited to the contractions, of the tail muscles in Appendicularia, of the muscle-bands of the body-wall in Doliolum, by which swimming is effected. The mode of obtaining food resembles that which has already been described in the case of the Pelecypoda (Vol. I. p. 640), the currents which subserve respiration also bringing in microscopic organic particles to the mouth.

Affinities.—That the Urochorda are degenerate descendants of primitive Chordates admits of little doubt; the history of the development of the Ascidians, taken in connection with the occurrence of permanently chordate members of the group (Appendicularia and its allies), is quite sufficient to point to this conclusion. But the degree of degeneration which the class has undergone—the point in the line of development of the higher Chordata from which it diverged—is open to question. According to one view the Urochorda are all extremely degenerate, and have descended from ancestors which had all the leading features of the Craniata; according to another the ancestors of the class were much lower than any existing Craniate—lower in the scale than even Amphioxus—and had not yet acquired the distinctive higher characteristics of the Craniates. The nearest existing ally of the Urochorda among lower forms is probably Balanoglossus. The similarity in the character of the pharynx or anterior segment of the enteric canal, perforated by branchial apertures, is alone sufficient to point to such a connection; and further evidence is afforded by the occurrence of a notochord in both, and by the similarity in the development of the central part of the nervous system. But the alliance is by no means a close one, and Balanoglossus and its allies can only be looked upon as very remotely connected with the stock from which the Urochorda are descended.

SUB-PHYLUM III.—VERTEBRATA.

We have seen that the fundamental characters of the Chordata are the presence of a notochord, of a dorsal hollow nervous system, and of a pharynx perforated by apertures or gill-slits. In none of the lower Chordata, however, are these structures found in a

typical condition, at least in the adult. In Balanoglossus, Cephalodiscus, and Rhabdopleura, the "notochord" is rudimentary, and in nearly all Tunicata it is present only in the embryo. In Rhabdopleura the gill-slits are absent, and in that genus as well as in Cephalodiscus and the adult Tunicata the nervous system is represented by a single solid nerve-centre or ganglion, the neurocœle being absent. In Balanoglossus, moreover, there is a ventral as well as a dorsal nerve-cord, and it is only in the anterior portion of the latter that the neurocœle is represented.

In the Vertebrata, on the other hand, what have been called the three fundamental chordate peculiarities are fully and clearly developed. There is always a distinct notochord extending as a longitudinal axis throughout the greater part of the elongated body, and either persisting throughout life, or giving place to an articulated *vertebral column* or backbone. The central nervous system remains throughout life in the form of a dorsal nerve-tube or *neuron*, containing a longitudinal canal or neurocœle. And the pharynx is always perforated, either throughout life or in the embryonic condition, by paired branchial apertures or gill-slits. In addition to these characters the mouth is ventral and anterior, the anus ventral and posterior; the muscular layer of the body-wall is segmented, and the renal organs arise as meso-nephridia. Moreover there is always an important digestive gland, the *liver*, developed as a hollow outpushing of the gut, and distinguished by the fact that the blood from the intestine circulates through it before passing into the general current, thus giving rise to what is called the *hepatic portal system* of blood vessels.

There are two primary sub-divisions of Vertebrata of very unequal size.

DIVISION A.—ACRANIA.

Including only the little fish-like Lancelets.

DIVISION B.—CRANIATA.

Including Fishes, Amphibians, Reptiles, Birds, and Mammals.

DIVISION A.—ACRANIA.

The division Acrania contains a single family, the *Branchiostomidæ*, containing two genera, *Branchiostoma* (usually known by the name of one of its sub-genera, *Amphioxus*), and *Asymmetron*. The differences between the genera and species are comparatively insignificant, and the following description will deal exclusively with the best known and most thoroughly investigated species, the Lancelet or Amphioxus, *Amphioxus lanceolatus*, found in the English Channel, the North Sea, and the Mediterranean.

Amphioxus is a small transparent animal, occurring near the shore and burrowing in sand; its length does not exceed 5·8 cm. or less than two inches. Its form will be obvious from Fig. 696 and from the transverse sections, Fig. 697, *A* and *B*. The body is elongated, pointed at either end, and compressed. The anterior two-thirds is roughly triangular in transverse section, presenting right and left sides, inclined towards one another, above, and a convex ventral surface. The posterior third is nearly oval in section, the right and left sides meeting above and below in a somewhat sharp edge.

Extending along the whole of the dorsal border is a median longitudinal fold, the *dorsal fin* (*dors. f.*): this is continued round the posterior end of the body and extends forwards, as the *ventral fin* (*vent. f.*), as far as the spot where the oval gives place to the triangular transverse section. The portion of the continuous

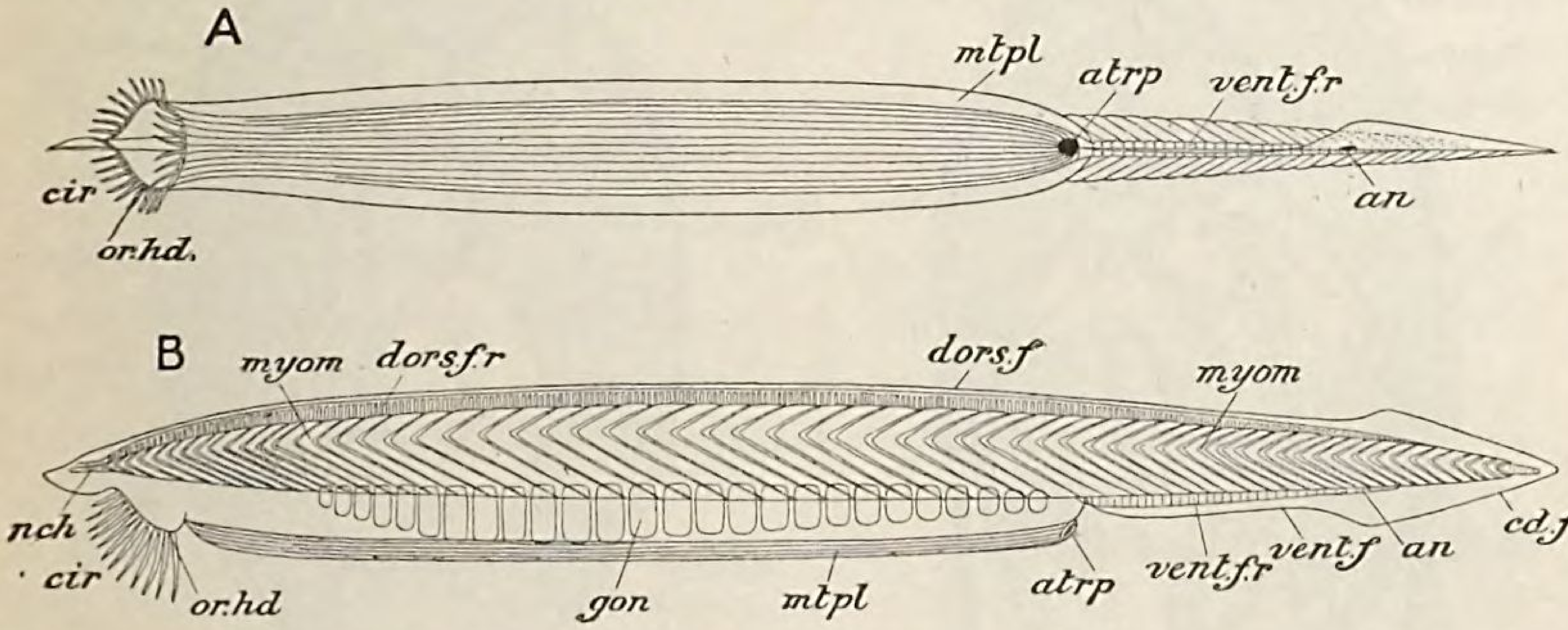


FIG. 696.—**Amphioxus lanceolatus.** A, ventral, B, side view of the entire animal. *an.* anus; *atrp.* atriopore; *cd. f.* caudal fin; *cir.* cirri; *dors. f.* dorsal fin; *dors. f. r.* dorsal fin rays; *gon.* gonads; *mtpl.* metapleure; *myom.* myomeres; *nch.* notochord; *or. hd.* oral hood; *vent. f.* ventral fin; *vent. f. r.* ventral fin rays. (After Kirkaldy.)

median fold which extends round the pointed posterior extremity of the body is somewhat wider than the rest and may be distinguished as the *caudal fin* (*cd. f.*). In the anterior two-thirds of the body there is no median ventral fin, but at the junction of each lateral with the ventral surface is a paired longitudinal fold, the *metapleure* (*mtpl.*), which extends forwards to the oral hood mentioned in the next paragraph.

Below the pointed anterior extremity is a large median aperture surrounded by a frill-like membrane, the *oral hood* (*or. hd.*), the edge of which is beset with numerous tentacles or *cirri* (*cir.*). The oral hood encloses a cup-shaped cavity or *vestibule*, at the bottom of which is the *mouth* (Fig. 698, *mth*). Immediately in front of the anterior termination of the ventral fin and partly enclosed by the metapleures is a rounded aperture of considerable size, the *atriopore* (*atrp*), and a short distance from the posterior extremity of the body is the *anus* (*an*), placed unsymmetrically on the left side of

the ventral fin. The post-anal portion of the body is distinguished as the *tail*.

Amphioxus ordinarily lives with the greater part of the body buried in sand, only the anterior end with the expanded oral hood protruding. It also swims in the vertical position, and frequently lies on one side on the sand: it burrows, head foremost, with great rapidity. A current of water is constantly passing in at the mouth and out at the atriopore.

Body-wall.—The body is covered with an *epidermis* (Fig. 697) formed of a single layer of columnar epithelial cells, some of which

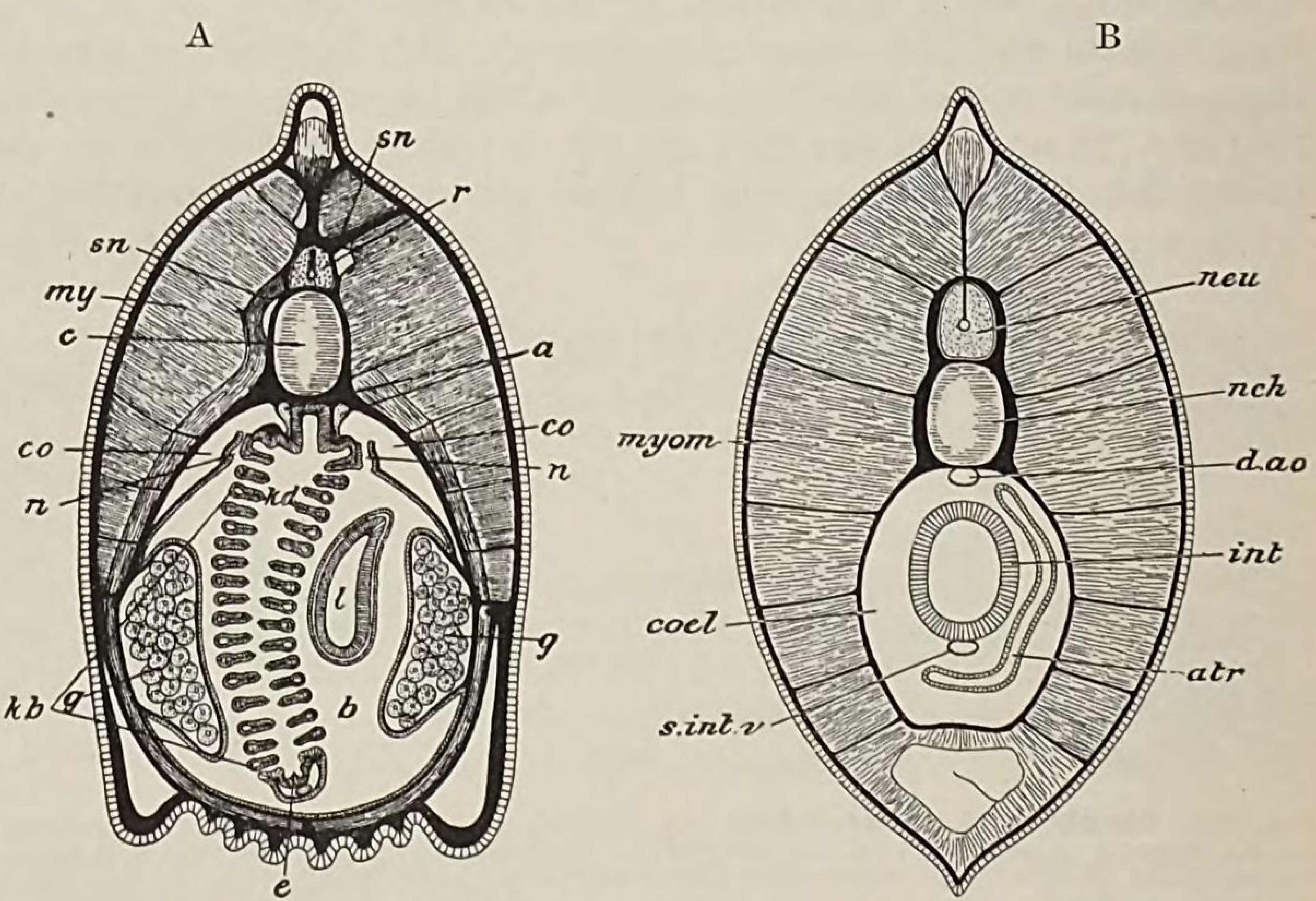


FIG. 697.—**Amphioxus lanceolatus.** A, transverse section of the pharyngeal region. *a*, dorsal aorta; *b*, atrium; *c*, notochord; *cö.* cœlome; *e.* endostyle; *g.* gonad; *kb*, branchial lamellæ; *kd*, pharynx; *l.* liver; *my.* myomere; *n*, nephridium; *r*, neuron; *sn.* spinal nerves; *sp.* gill-slits. B, transverse section of the intestinal region. *atr.* atrium; *cæl.* cœlome; *d. ao.* dorsal aorta; *int.* intestine; *myom.* myomere; *nch.* notochord; *neu.* neuron; *s. int. v.* sub-intestinal vein. (A, from Hertwig, after Lankester and Boveri; B, partly after Rolph.)

are provided with sensory hairs. The epithelium of the buccal cirri presents at intervals regular groups of sensory cells, some of them bearing stiff sensory hairs, others cilia. Beneath the epidermis is the *dermis*, formed mainly of gelatinous connective tissue.

The *muscular layer* (*my*, *myom.*) is remarkable for exhibiting metameric segmentation. It consists of a large number—about sixty—of muscle-segments or *myomeres*, separated from one another by partitions of connective tissue, the *myocommas*, and having the appearance, in a surface view, of a series of very open V's with their apices directed forwards (Figs. 696 and 698). Each myomere

is composed of numerous flat, striated *muscle plates*, arranged longitudinally, so that each is attached to two successive myocommas. In virtue of this arrangement the body can be bent from side to side with great rapidity. The myomeres of the right and left sides of the body are not opposite to one another, but have an alternate arrangement. A special set of *transverse muscles* (Fig. 697, A), extends across the ventral surface of the anterior two-thirds of the body, lying in the floor of the atrial cavity presently to be described.

One striking and characteristic feature of the muscular layer of the body-wall is the immense thickness of its dorsal portion. In the higher Worms and many other Invertebrates the muscles form a layer of approximately equal thickness surrounding the body-cavity, which contains, amongst other organs, the central nervous system. In Vertebrates, on the other hand, the dorsal body-wall is greatly thickened, and in it are contained both the nervous system and the notochord.

Skeleton.—The chief of the skeletal or supporting structures of the Lancelet is the *notochord* (Figs. 697 and 698, *nch.*), a cylindrical rod, pointed at both ends, and extending from the anterior to the posterior end of the body in the median plane. It lies immediately above the enteric tract and between the right and left myomeres. It is composed of a peculiar form of cellular tissue, known as *notochordal tissue*, formed of large vacuolated cells extending from side to side of the notochord, and having the nuclei confined to its dorsal and ventral regions. Around these cells is a *notochordal sheath* of connective tissue, which is produced dorsally into a canal for the nervous system. The notochord, like the parenchyma of plants, owes its resistent character to the vacuoles of its component cells being tensely filled with fluid, a condition of turgescence being thus produced.

The oral hood is supported by a ring (Fig. 698, *sk.*) of cartilaginous consistency, made up of separate rod-like pieces arranged end to end, and corresponding in number with the cirri. Each piece sends an offshoot into the cirrus to which it is related, furnishing it with a skeletal axis.

The pharynx is supported by delicate oblique rods of a chitinoid material, the *gill-rods* (*br. r.*). These will be most conveniently discussed in connection with the pharynx itself. The dorsal fin is supported by a single series, and the ventral fin by a double series, of *fin-rays* (*dors. f. r.*, *vent. f. r.*), short rods of connective tissue, each contained in a cavity or *lymph space*.

Digestive and Respiratory Organs.—The mouth (*mth.*), as already mentioned, lies at the bottom of the vestibule or cavity of the oral hood (*or. hd.*). It is a small circular aperture surrounded by a membrane, the *velum* (*vl.*) which acts as a sphincter, and has its free edge produced into a number of *velar tentacles* (*vl. t.*).

The mouth leads into the largest section of the enteric canal, the *pharynx* (*ph.*), a high, compressed chamber extending through the anterior half of the body. Its walls are perforated by more than a hundred pairs of narrow oblique clefts, the *gill-slits* or *branchial apertures* (*br. cl.*), which place the cavity of the pharynx in communication with the atrium (see below). From the posterior end of the pharynx goes off the tubular *intestine* (*int.*) which extends backwards, almost in a straight line to the anus.

On the ventral wall of the pharynx is a longitudinal groove, the *endostyle* (Fig. 697, A, *e.*), lined by ciliated epithelium containing groups of gland-cells. Like the homologous organ in Ascidia (p. 14), the glands secrete a cord of mucus in which food particles are entangled and carried by the action of the cilia to the intestine. A somewhat similar structure, the *epi-pharyngeal groove*, extends along the dorsal aspect of the pharynx: its sides are formed by ciliated cells, which, at the anterior end of the groove, curve downwards, as the *peri-pharyngeal bands*, and join the anterior end of the endostyle.

From the ventral region of the anterior end of the intestine is given off a blind pouch, the *liver* (*lr.*) or *hepatic cæcum*, which extends forwards, to the right of the pharynx: it is lined with glandular epithelium and secretes a digestive fluid.

The *gill-slits* (*br. cl.*) are long, narrow clefts, nearly vertical in the expanded condition, but very oblique in preserved and contracted specimens—hence the fact that a large number of clefts always appear in a single transverse section (Fig. 697, A, *sp.*). The clefts are more numerous than the myomeres in the adult, but correspond with them in the larva: hence they are fundamentally metameric, but undergo an increase in number as growth proceeds.

The *branchial lamellæ* (Fig. 698, *br. sep.*, Fig. 697, A, *kb.*) or portions of the pharyngeal wall separating the clefts from one another, are covered by an epithelium which is for the most part endodermal in origin, and composed of greatly elongated and ciliated cells. On the outer face of each lamella, however, the cells are shorter and not ciliated, and are, as a matter of fact, portions of the epithelial lining of the atrium, and of ectodermal origin. Each lamella is supported towards its outer edge by one of the chitinoid *branchial rods* (*br. r.*) already referred to. These are narrow bars united with one another dorsally by loops, but ending below in free extremities which are alternately simple and forked. The forked bars are the *primary* (*br. r. 1*), those with simple ends the *secondary* (*br. r. 2*) *branchial rods*, and the lamellæ in which they are contained are similarly to be distinguished as *primary lamellæ* (*br. sep. 1*) and *secondary* or *tongue lamellæ* (*br. sep. 2*). In the young condition the two clefts between any two primary lamellæ are represented by a single aperture: as development proceeds a down-

growth takes place from the dorsal edge of the aperture, forming, as in Balanoglossus (p. 3), a *tongue* which extends downwards, dividing the original cleft into two, and itself becoming a secondary lamella. A further complication is produced by the formation of transverse *branchial junctions* connecting the primary septa with one another at tolerably regular intervals.

The Atrium.—The gill-clefts lead into a wide chamber occupying most of the space between the body-wall and the pharynx and called the *atrium* (Fig. 698, *atr.*; Fig. 697, A, *b.*). It is crescentic in section, surrounding the ventral and lateral regions of the pharynx, but not its dorsal portion. It ends blindly in front; opens externally, behind the level of the pharynx, by the atriopore (*atrp.*); and is continued backwards by a blind, pouch-like extension (*atr'.*) lying to the right of the intestine (Fig. 697, B, *atr.*). The whole cavity is lined by an atrial epithelium of ectodermal origin. As in Ascidia, the cilia lining the gill-clefts produce a current setting in at the mouth,

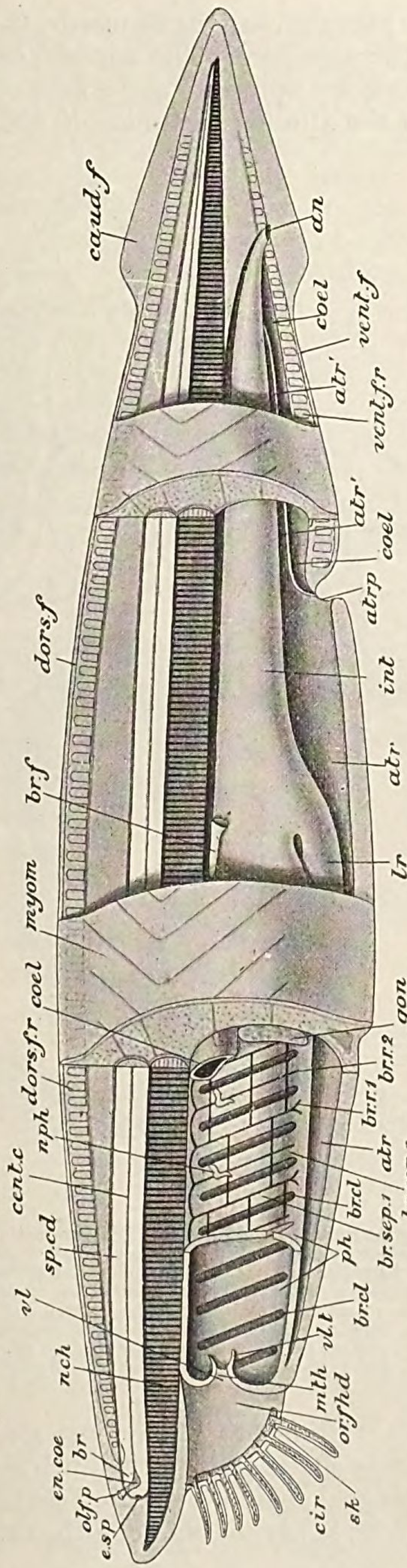


FIG. 698.—Diagram of the anatomy of **Amphioxus.** *an.* anus; *atr.* atrium; *atr'.* its posterior prolongation; *atrp.* atriopore; *br.* brain; *br. cl* branchial clefts; *br. f.* brown funnel; *br. sep. 1*, primary; *br. sep. 2*, secondary branchial lamella; *br. r. 1*, primary; *br. r. 2*, secondary branchial rod; *caud. f.* caudal fin; *cent. c.* central canal; *cir.* cirri; *cœl.* cœlome; *dors. f.* dorsal fin; *dors. f. r.* dorsal fin-ray; *en. cœ.* encephalocœle; *e. sp.* eye-spot; *gon.* gonad; *int.* intestine; *lr.* liver; *mth.* mouth; *myom.* myomeres; *nch.* notochord; *nph.* nephridia; *olf. p.* olfactory pit; *or. f. hd.* oral hood; *ph.* pharynx; *sk.* skeleton of oral hood and cirri (dotted); *sp. cd.* spinal cord; *vent. f.* ventral fin; *vent. f. r.* ventral fin-ray; *vel.* velum; *vl. t.* velar tentacles.

entering the pharynx, passing thence by the gill-slits into the atrium, and out at the atriopore. The current, as in Tunicata and Balanoglossus, is both a respiratory and a food current, the animal feeding passively on the minute organisms in the surrounding water.

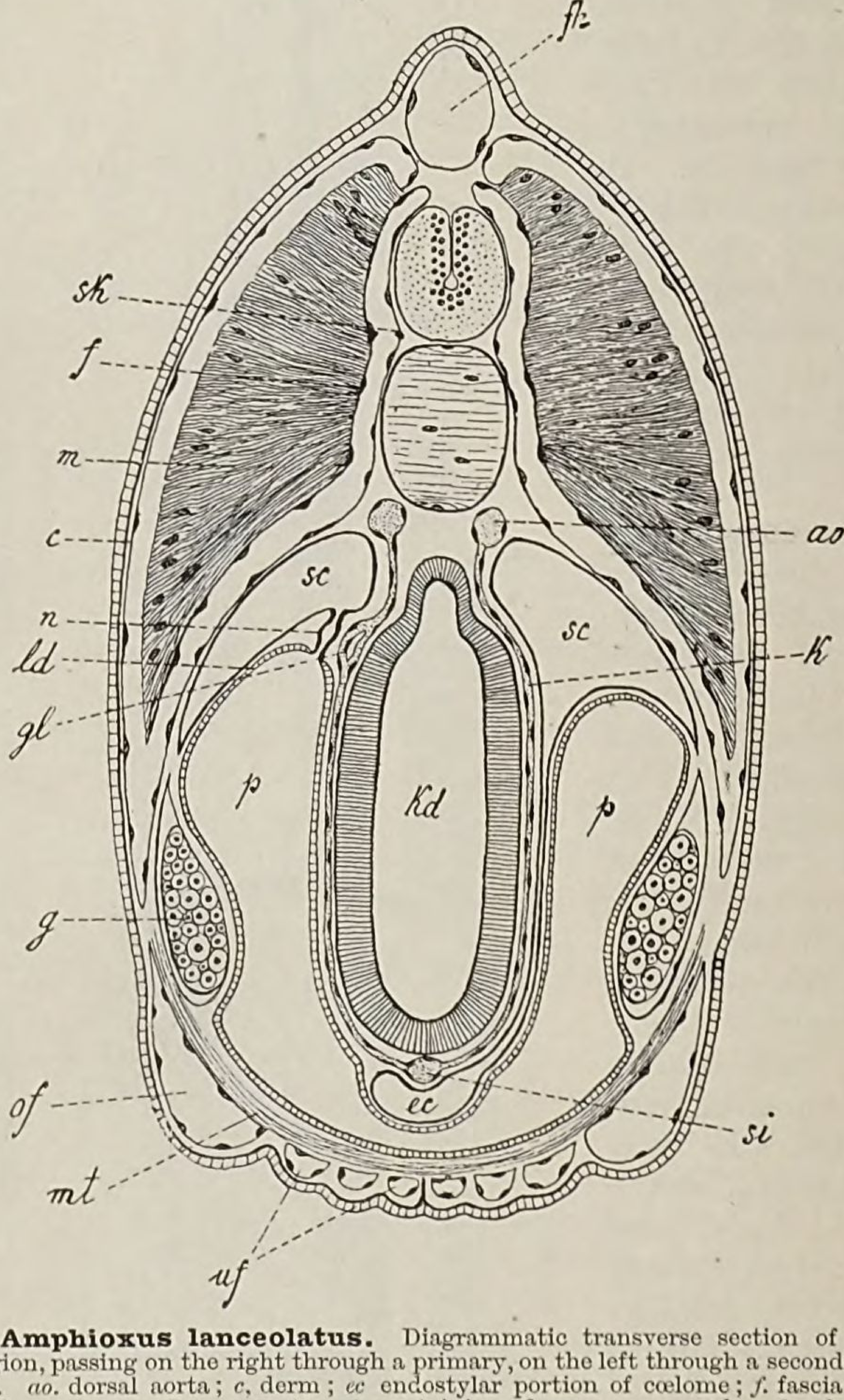


FIG. 699.—**Amphioxus lanceolatus.** Diagrammatic transverse section of the pharyngeal region, passing on the right through a primary, on the left through a secondary branchial lamella. *ao.* dorsal aorta; *c*, derm; *ec* endostylar portion of cœlome; *f.* fascia or investing layer of myomere; *fh*, compartment containing fin-ray; *g.* gonad; *gl.* glomerulus; *k*, branchial artery; *kd*, pharynx; *ld*, combined atrial and cœlomic wall (ligamentum denticulatum); *m.* myomere; *mt.* transverse muscle; *n.* nephridium; *of*, metapleural lymph-space; *p*, atrium; *sc*, cœlome; *si*, ventral aorta; *sk*, sheath of notochord and neuron; *uf*, spaces in ventral wall. (From Korschelt and Heider, after Boveri and Hatschek.)

Cœlome.—Owing to the immense size of the atrium the body cavity, which is a true cœlome, is much reduced. It is represented, in the pharyngeal region, by paired cavities (Fig. 698, *cœl.*, Fig. 697, A, *cö.*, Fig. 699, *sc.*) lying one on either side of the dorsal region of

the pharynx above the atrium, and connected by narrow canals in the primary branchial lamellæ (Fig. 699, right side), with a median longitudinal space below the endostyle (Fig. 699, *ec.*). In the intestinal region it is much reduced on the right side, being displaced by the backward extension of the atrium (Fig. 697, B, *atr.*, Fig. 698, *atr'.*), but is well developed on the left side: a forward extension of it surrounds the liver (Fig. 697, A, *l.*). The whole series of spaces is lined by cœlomic epithelium.

Blood-System.—The blood-vessels of Amphioxus are all of one kind, but, owing to certain undoubted homologies with the more complex vessels of the Craniata (see below), some of them receive the name of *arteries*, others of *veins*.

Lying in the ventral wall of the pharynx, below the endostyle, is a median longitudinal vessel, the *ventral aorta* (Fig. 700, *v. ao*, Fig. 699, *si.*); it is contractile and drives the blood forwards. From it are given off, on each side, lateral branches, the *afferent*

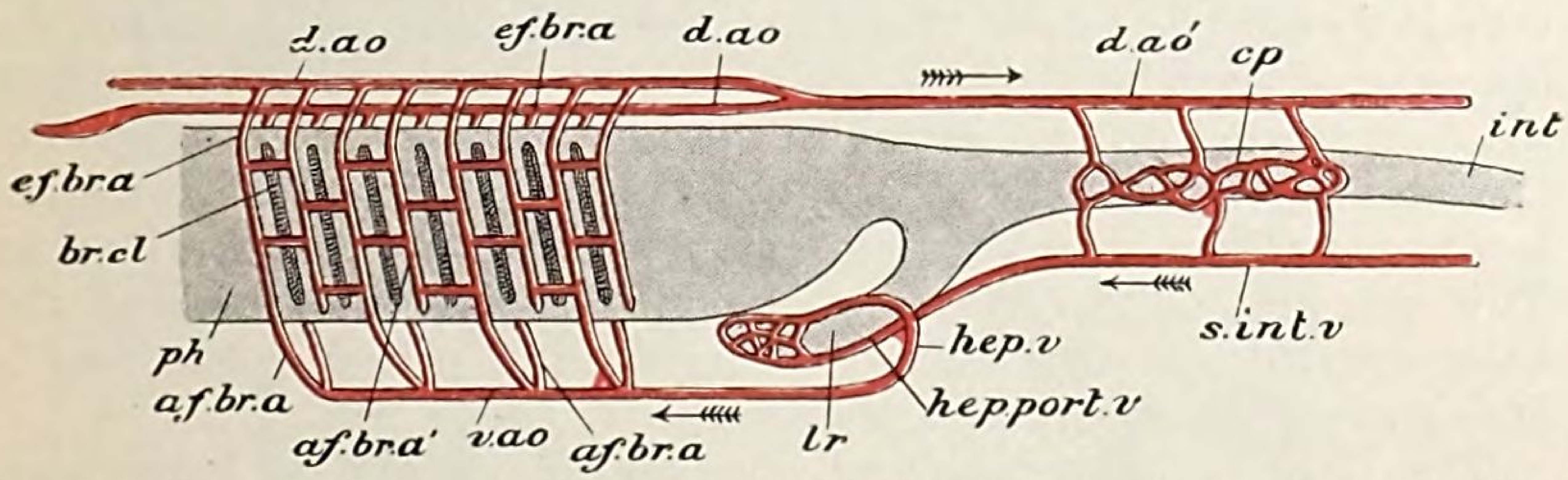


FIG. 700.—Diagram of the vascular system of **Amphioxus**. *af. br. a.* afferent branchial arteries; *cp.* intestinal capillaries; *d. ao.* paired dorsal aortæ; *d. ao.'* median dorsal aorta; *ef. br. a.* efferent branchial arteries; *hep. port. v.* hepatic portal vein; *hep. v.* hepatic vein; *int.* intestine; *lr.* liver; *ph.* pharynx; *s. int. v.* sub-intestinal vein.

branchial arteries (Fig. 700, *af. br. a.*; Fig. 699, *k*), which pass up the primary branchial lamellæ and communicate by cross-branches with similar vessels (*af. br. a'.*) in the secondary or tongue lamellæ. The blood is exposed, while traversing these vessels, to the aërating influence of the respiratory current, and leaves the branchial lamellæ dorsally by *efferent branchial arteries* (*ef. br. a.*) which open on each side into paired longitudinal vessels, the *right* and *left dorsal aortæ* (*d. ao.*), lying one on each side of the epipharyngeal groove. Anteriorly both dorsal aortæ are continued forwards to the region of the snout, the right being much dilated; posteriorly they unite with one another, behind the level of the pharynx, into an *unpaired dorsal aorta* (*d. ao'.*), which extends backwards in the middle line, immediately below the notochord and above the intestine.

The unpaired dorsal aorta sends off branches to the intestine, in the walls of which they break up to form a network of microscopic vessels or *capillaries* (*cp.*). From these the blood is collected and

poured into a median longitudinal vessel, the *sub-intestinal vein* (Figs. 697, B, and 700, *s. int. v.*), lying beneath the intestine: in this trunk the blood flows forwards, and, at the origin of the liver, passes insensibly into a *hepatic portal vein* (*hep. port. v.*), which extends along the ventral side of the liver and breaks up into capillaries in that organ. From the liver the blood makes its way into a *hepatic vein* (*hep. v.*), which extends along the dorsal aspect of the digestive gland, and, turning downwards and forwards, joins the posterior end of the ventral aorta.

It will be seen that the vascular system of Amphioxus consists essentially of (*a*) a dorsal vessel represented by the paired and unpaired dorsal aortæ, (*b*) a ventral vessel represented by the sub-intestinal vein and the ventral aorta, and (*c*) commissural vessels represented by the afferent and efferent branchial arteries and the intestinal capillaries. So far the resemblance to the vascular system of Annulata is tolerably close; but two important differences are to be noted. The blood in the ventral vessel travels forwards, that in the dorsal vessel backwards—the precise opposite of what occurs in Worms, and the ventral vessel is broken up, as it were, into two parts, by the interposition in its course of the capillaries of the liver, so that all the blood from the intestine has to pass through that organ before reaching the ventral aorta. This passage of the intestinal blood through the vessels of the liver constitutes what is called the *hepatic portal system*, and is eminently characteristic of Vertebrata.

The *blood* is colourless, and appears to contain no leucocytes. It is not confined to the true blood vessels just described, but occurs also in certain cavities or *lymph-spaces*, the most important of which are the cavities in the dorsal and ventral fins containing the fin-rays (Fig. 699, *fh.*), and paired canals in the metapleures (*of.*).

Excretory Organs.—The principal organs of excretion are about ninety pairs of peculiarly modified *nephridia* (Fig. 698, *neph.*) situated above the pharynx and in relation with the main cœlomic cavities. Each nephridium (Fig. 701) is a bent tube consisting of an anterior vertical and a posterior horizontal limb. The vertical limb opens by a wide aperture into the cœlome: the horizontal limb has several cœlomic apertures, one at its posterior end, the others on its dorsal surface. On the ventral surface of the horizontal limb, opposite a secondary branchial lamella, is a single aperture bearing long cilia and opening into the atrium: this corresponds with the nephridiopore or external apertures of the typical nephridium. With the cœlomic apertures are connected peculiar thread-like cells with knobbed extremities.

An excretory function has also been assigned to a single pair of organs called the *brown funnels* (Fig. 698, *br. f.*), also situated on the dorsal aspect of the pharynx at its posterior end. Their wide, backwardly directed ends open into the atrium; their

narrow anterior ends probably communicate with the cœlome. There are also groups of columnar excretory cells on the floor of the atrium.

Nervous System.—The central nervous system is a rod-like organ the *neuron* or *dorsal nerve-tube* (Fig. 697, A, *n.*; B. *neu.*, Figs. 698, 699), contained within and completely filling a median longitudinal *neural canal* which lies immediately above the notochord. It is roughly triangular in transverse section : anteriorly it ends abruptly some distance behind the anterior end of the

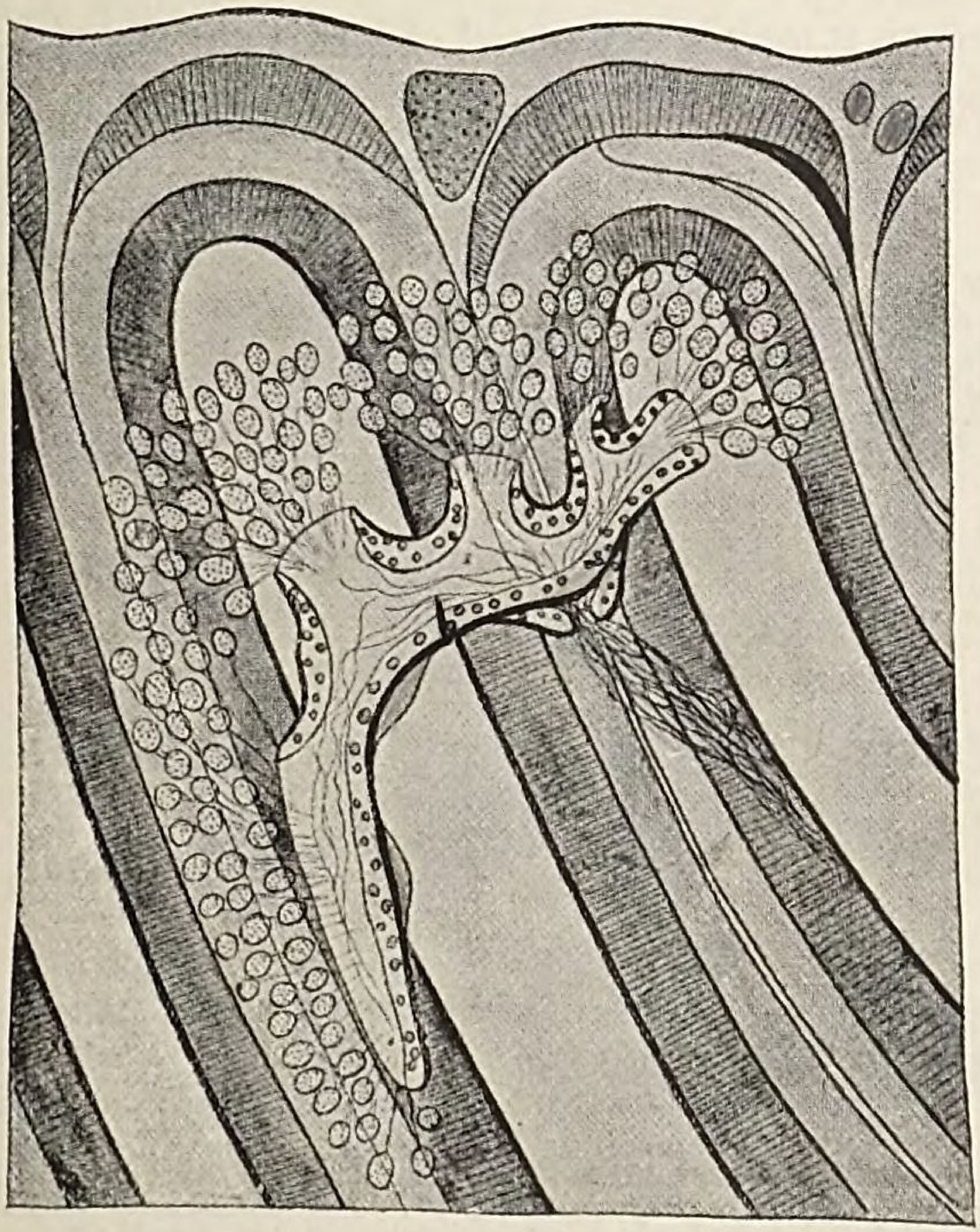


FIG. 701.—**Amphioxus lanceolatus.** A, nephridium of the left side with part of the wall of the pharynx. (From Willey, after Boveri.)

notochord, while posteriorly it tapers to a point over the hinder end of the latter. It is traversed by an axial cavity, the *neurocœle* (Fig. 698, *cent. c.*), connected with the mid-dorsal region by a longitudinal cleft. At the fore-end of the nerve-tube the neurocœle becomes greatly dilated, forming a considerable cavity, the *encephalocœle* or *cerebral ventricle* (Fig. 698, *en. cœ.*, Fig. 702, *cv.*), and a little behind this the dorsal fissure widens out above to form a trough-like *dorsal dilatation* (*dil.*) covered only by the delicate connective tissue sheath which invests the whole nerve-

tube. The anterior end of the neuron, containing these two cavities, is to be looked upon as the *brain*, although not distinguishable externally from the remaining portion or *spinal cord*.

The anterior and dorsal region of the brain is produced into a small hollow pointed pouch which comes into relation with the olfactory organ and is called the *median olfactory lobe*. In its posterior and ventral region a depression has been described which appears to correspond with the *infundibulum* of the Craniata (*vide infra*).

The neuron is mainly composed of longitudinal nerve-fibres with abundant nerve cells mostly grouped around the neurocœle. At

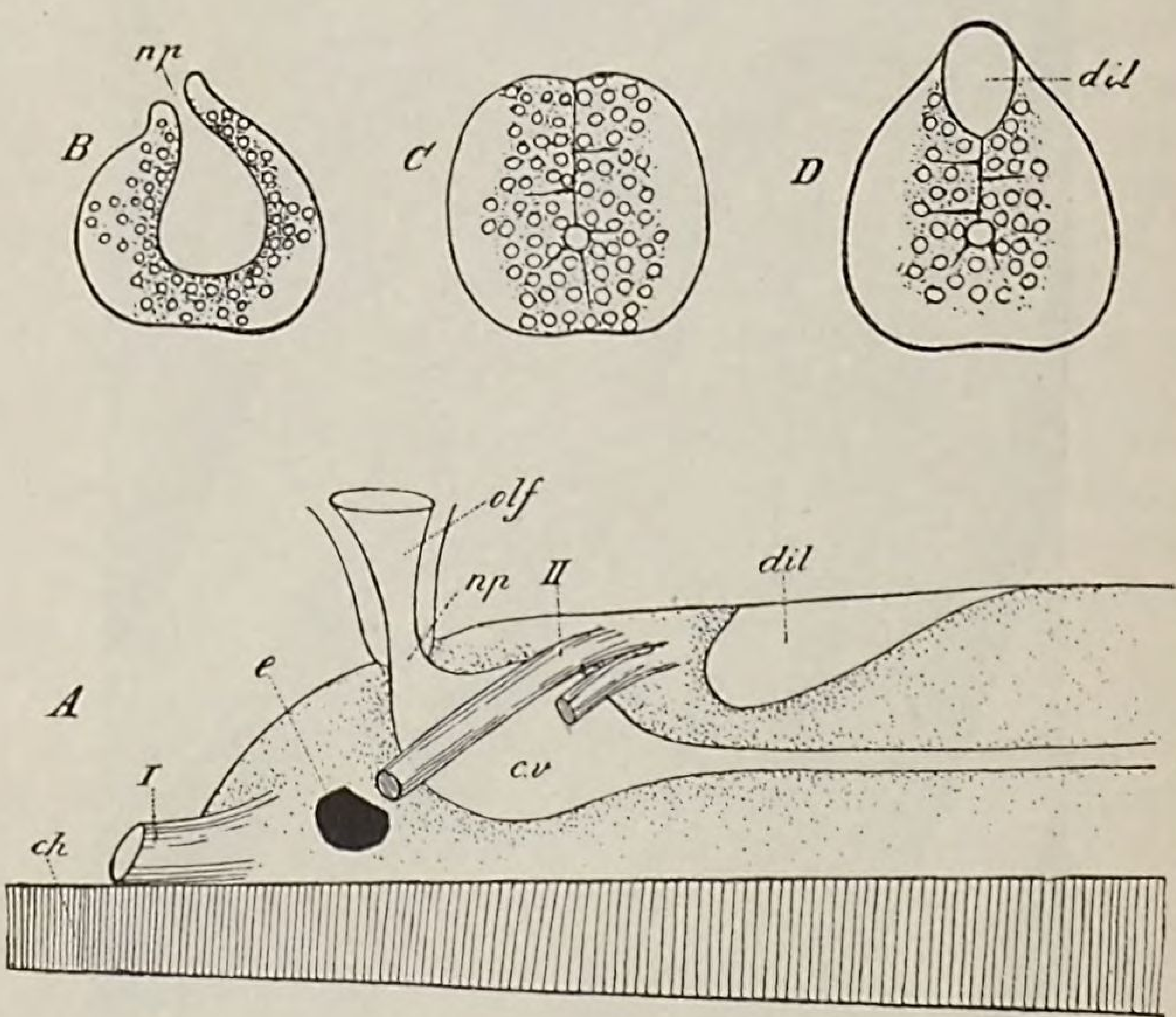


FIG. 702.—**Amphioxus lanceolatus.** A, brain and cerebral nerves of a young specimen; B, transverse section through neuropore; C, behind cerebral ventricle; D, through dorsal dilatation. *ch.* notochord; *cv.* cerebral ventricle; *dil.* dorsal dilatation; *e.* eye-spot; *np.* neuropore; *olf.* olfactory pit; *I*, *II*, cerebral nerves. (From Willey, after Hatschek.)

intervals *giant nerve-cells* occur, multipolar cells of immense proportional size, connected with nerve-fibres of unusual size, the *giant fibres*. The latter appear to correspond with the giant fibres of Chætopods (Vol. I. p. 438) which, however, have no nervous function and are mere supporting structures.

The peripheral nervous system consists of the *nerves* given off from the neuron. They are divisible into two sets, the first consisting of two pairs of *cerebral nerves* (Fig. 702, I. and II.) arising from the brain, the second of a large number of *spinal nerves* arising from the spinal cord. The cerebral nerves take their

origin in front of the first myomere, the first from the anterior extremity of the brain, the second from its dorsal region: they are both distributed to the snout, their branches being provided towards their extremities with numerous ganglia containing nerve-cells. The spinal nerves are segmentally arranged, and, in correspondence with the disposition of the myomeres, those of the right and left sides arise alternately, and not opposite one another (Fig. 703). In each segment there are two nerves on each side, a *dorsal nerve*, arising by a single root from the dorsal aspect of the spinal cord, and a *ventral nerve* arising by numerous separate fibres: the dorsal nerves supply the skin and the transverse muscles and are therefore both sensory and motor, the ventral nerves are purely motor, supplying the myomeres.

Sensory Organs.—At the level of the anterior end of the brain is a narrow ciliated depression, the *olfactory pit* (Fig. 702, *olf.*) opening externally on the left side of the snout and connected at its lower end with the median olfactory lobe. This structure is supposed to be an organ of smell: in the larva its cavity is in direct communication with the neurocœle through an aperture, the *neuropore* (*np.*), which becomes closed in the adult. There is some reason for thinking that the olfactory pit answers to the *hypophysis* or *pituitary body* of Urochorda and Craniata (pp. 17 and 96).

The organ of sight is an unpaired *pigment spot* (*e*) in the front wall of the brain: it is therefore a median *cerebral eye*. There is no lens or other accessory apparatus. Smaller pigment spots occur in the spinal cord throughout the greater part of its length, below the neurocœle. There is no trace of auditory organ. A peculiar structure, the *groove of Hatschek*, on the roof of the oral hood, is supposed to have a sensory function, and may be an organ of taste. Lastly, the sensory cells on the buccal cirri give those organs an important tactile function.

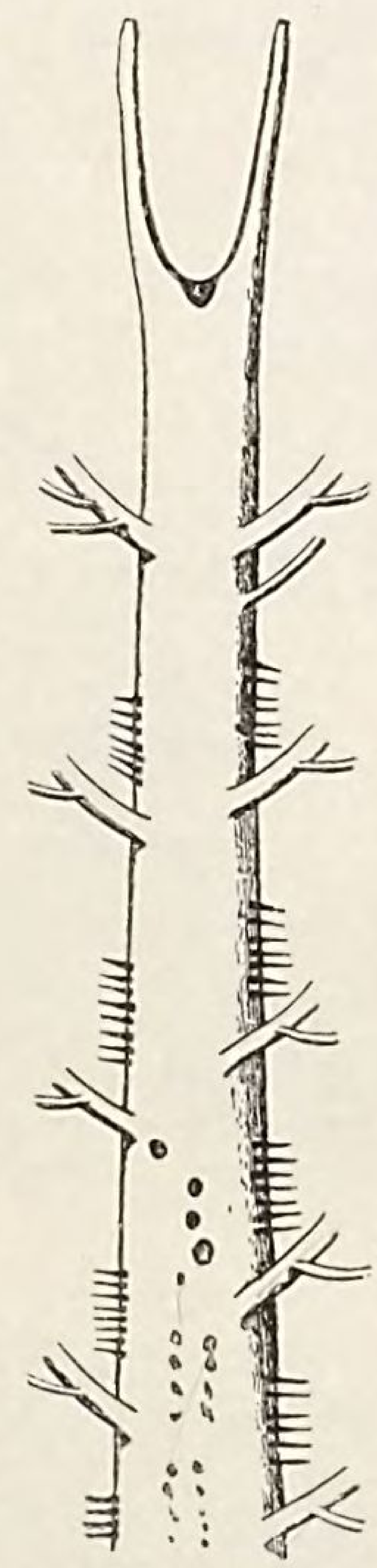


FIG. 703.—**Amphioxus lanceolatus.** Anterior portion of neuron from above, showing nerves. (From Willey, after Schneider.)

Reproductive Organs.—The sexes are separate, but there is no distinction, apart from the organs of reproduction, between male and female. The *gonads* (Fig. 698, *gon.*, Figs. 697, A, and 699, *g.*) are about twenty-six pairs of pouches arranged metamerically along the body-wall, and projecting into the atrium so as largely to fill up its cavity. The inner or mesial face of each pouch is

covered by atrial epithelium pushed inwards by the growth of the gonad; within this, and completely surrounding the reproductive organ, is a single layer of epithelium which is shown by development to be cœlomic. Hence each gonad is surrounded by a closed cœlomic sac.

When ripe the inner walls of the gonadic pouches burst, and the ova or sperms make their way into the atrium and thence

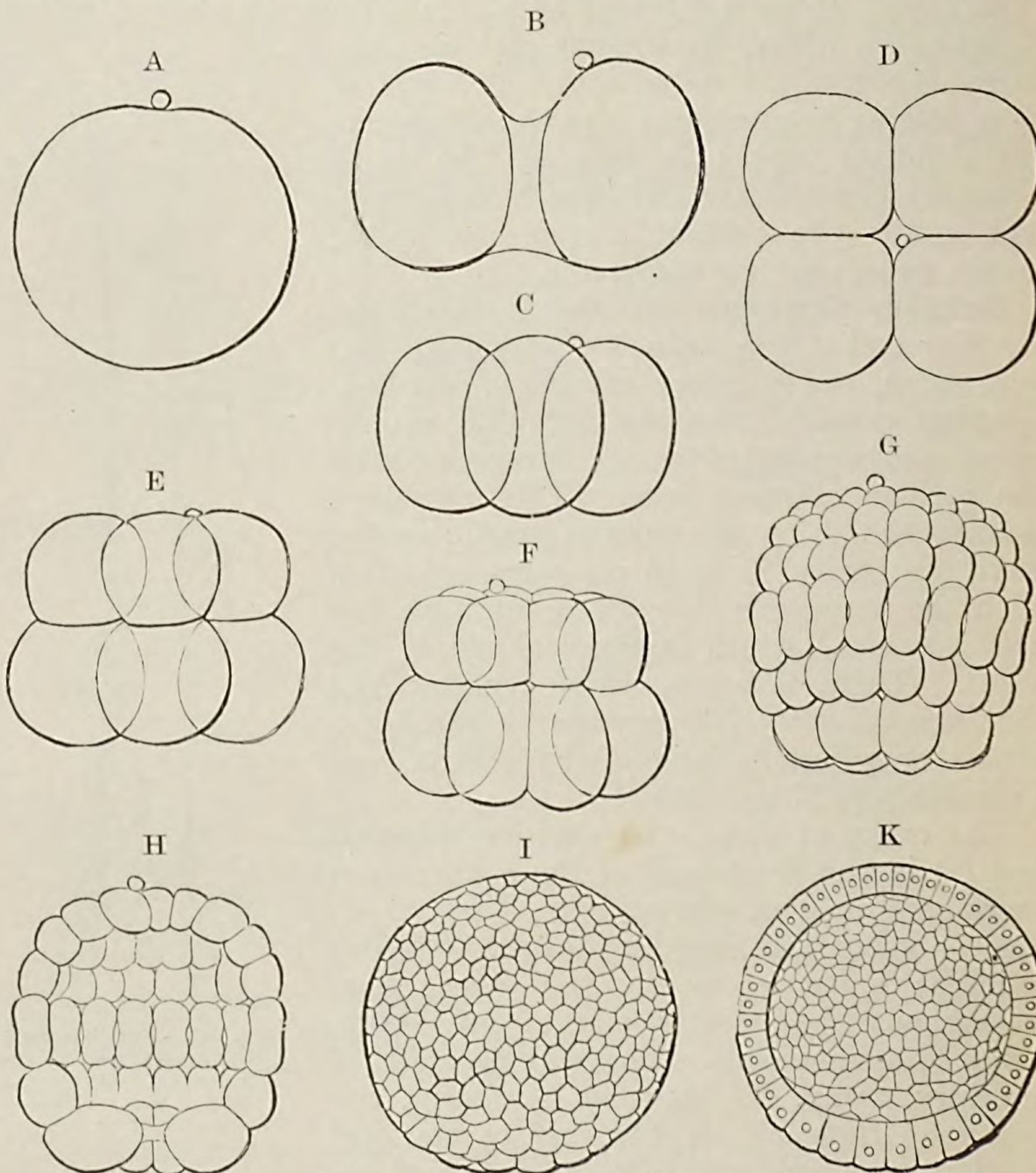


FIG. 704.—**Amphioxus lancelolatus.** Segmentation of the oosperm. D, the four-celled stage, (C) from above ; H, vertical section of G ; K, vertical section of the blastula stage I. (From Korschelt and Heider, after Hatschek.)

by the atriopore to the external water where impregnation takes place. The laid eggs are covered by a thin *follicular membrane*, formed of flattened cells.

Development.—Only one polar body has been observed (Fig. 704, A). After impregnation the follicular membrane separates

from the oosperm leaving a wide space around the latter. Segmentation is complete, there being very little yolk: it begins by a meridional cleft dividing the oosperm into two (B), and followed by a second cleft, also meridional, at right angles to the first (C, D). Next, an equatorial cleavage takes place, the embryo coming to be formed of eight cells (E), of which the four belonging to the upper hemisphere, distinguished by the presence of the polar cell, are smaller than the lower four. Further meridional and equatorial divisions take place, and the embryo becomes a *blastula* (I, K), enclosing a spacious blastocœle, and having the cells on its lower pole larger than the rest.

Invagination then takes place (Fig. 705, A), the lower pole of the blastula becoming gradually pushed in until the whole lower hemisphere is in complete contact with the upper hemisphere and the blastocœle obliterated (B). The *gastrula* thus formed

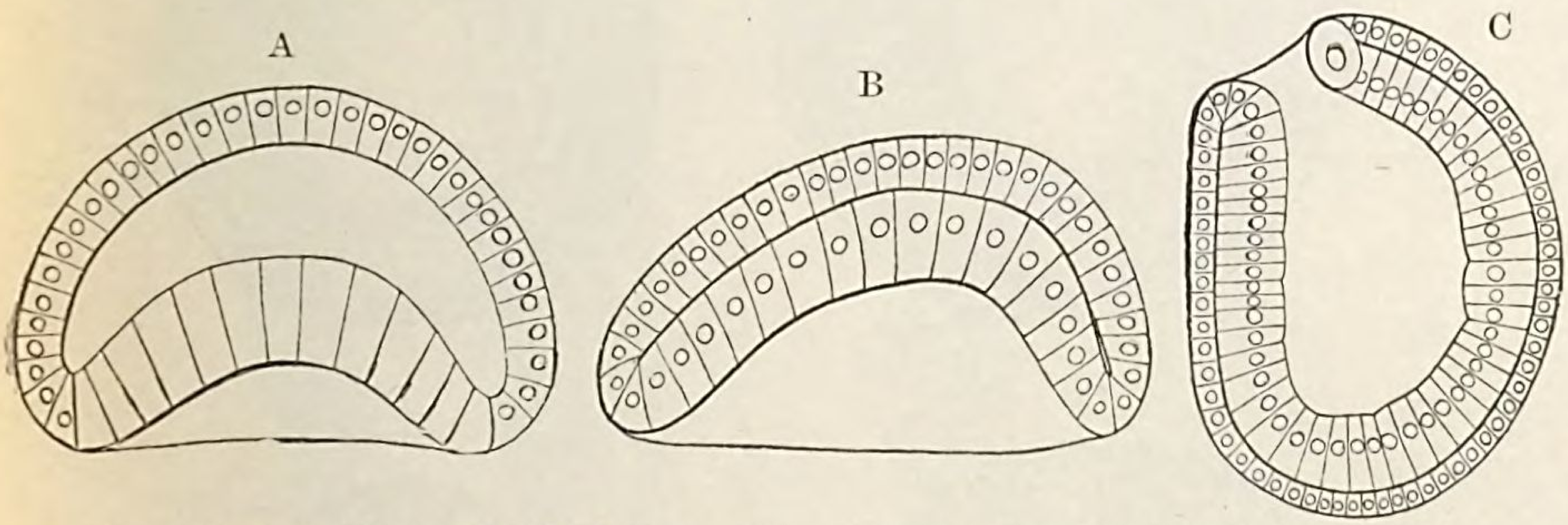


FIG. 705.—**Amphioxus lanceolatus.** Three stages in the formation of the gastrula (From Korschelt and Heider, after Hatschek.)

is at first basin-shaped, having a very wide blastopore, but its cavity gradually deepens, and the blastopore is reduced to a comparatively narrow aperture (C). At the same time the aspects of the body are marked out: the dorsal surface becomes flattened, the ventral convex; the blastopore marks the posterior end and is distinctly dorsal in position. Cilia are developed from the ectoderm cells and by their vibration cause the embryo to rotate within its membrane.

The ectoderm cells forming the median portion of the flattened dorsal surface now become differentiated and sink below the rest, giving rise to the *medullary plate* (Fig. 706, A, *mp*). The ordinary ectoderm cells on each side of this plate rise up as a pair of longitudinal *medullary folds* (*hb*), extend towards the middle line and unite (B, *hb*), covering over the medullary plate. The latter bends upwards at the sides so as to become trough-like instead of flat (C), and, its two sides coming in contact with one another above, the plate is converted into a tube, the *neuron* (D, *n*).

enclosing a central canal, the *neurocœle*, continued dorsally into a narrow cleft. The medullary folds extend behind the blastopore so that when they unite the latter aperture opens into the neurocœle by a *neurenteric canal* (Fig. 707, A, *cn*). Anteriorly the folds remain apart up to a late period so that the neurocœle opens externally in front by a wide aperture, the *neuropore* (Figs. 707, 708 and 709, *np*).

While the central nervous system is thus being formed, the endoderm sends out dorsally a paired series of offshoots, the

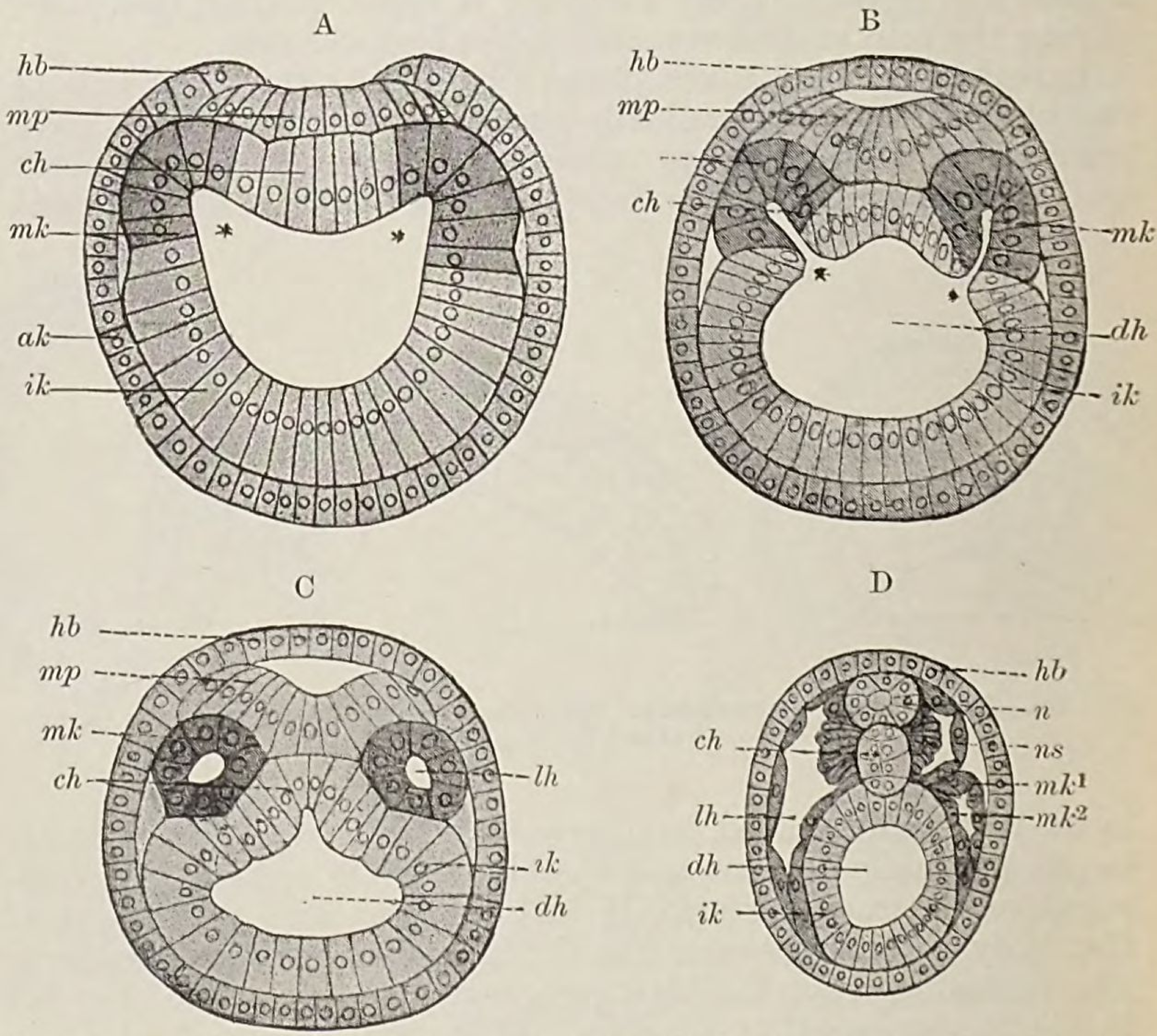


FIG 706.—**Amphioxus lanceolatus.** Four stages in the development of the notochord nervous system, and mesoderm. *ak*, ectoderm; *ch*, notochord; *dh*, cavity of archenteron; *hb*, ridge of ectoderm growing over medullary plate; *ik*, endoderm; *lh*, cœlome; *mk*, cœlomic pouch; mk^1, parietal layer of mesoderm; mk^2, visceral layer; *mp*. medullary plate; *n*. nerve-tube; *ns*, protovertebra. (From Korschelt and Heider, after Hatschek.)

cœlomic pouches (Fig. 706, *mk*) arranged metamerically. In this way segmentation is established, and it is at this period that the embryo ruptures its containing membrane and begins free existence. Before long the cœlomic pouches separate from the archenteron and take on the form of a series of closed *cœlomic sacs* (Fig. 706, C, D), lying between ectoderm and endoderm. From the walls of these sacs the mesoderm is derived, their

cavities become the cœlome, which is therefore an *enterocœle*, like that of Sagitta and the Echinodermata.

While the cœlomic sacs are in course of formation a median groove appears along the dorsal wall of the archenteron (Fig. 706, B, C, *ck*): it deepens, loses its tubular character, and becomes a solid rod, the *notochord* (D, *ck*), lying immediately beneath the nerve-tube. The ordinary endoderm cells soon unite beneath it and so shut it off from the archenteron. It will be seen that the notochord, like the neuron, never exhibits any trace of segmentation. At its first formation it stops short of the anterior

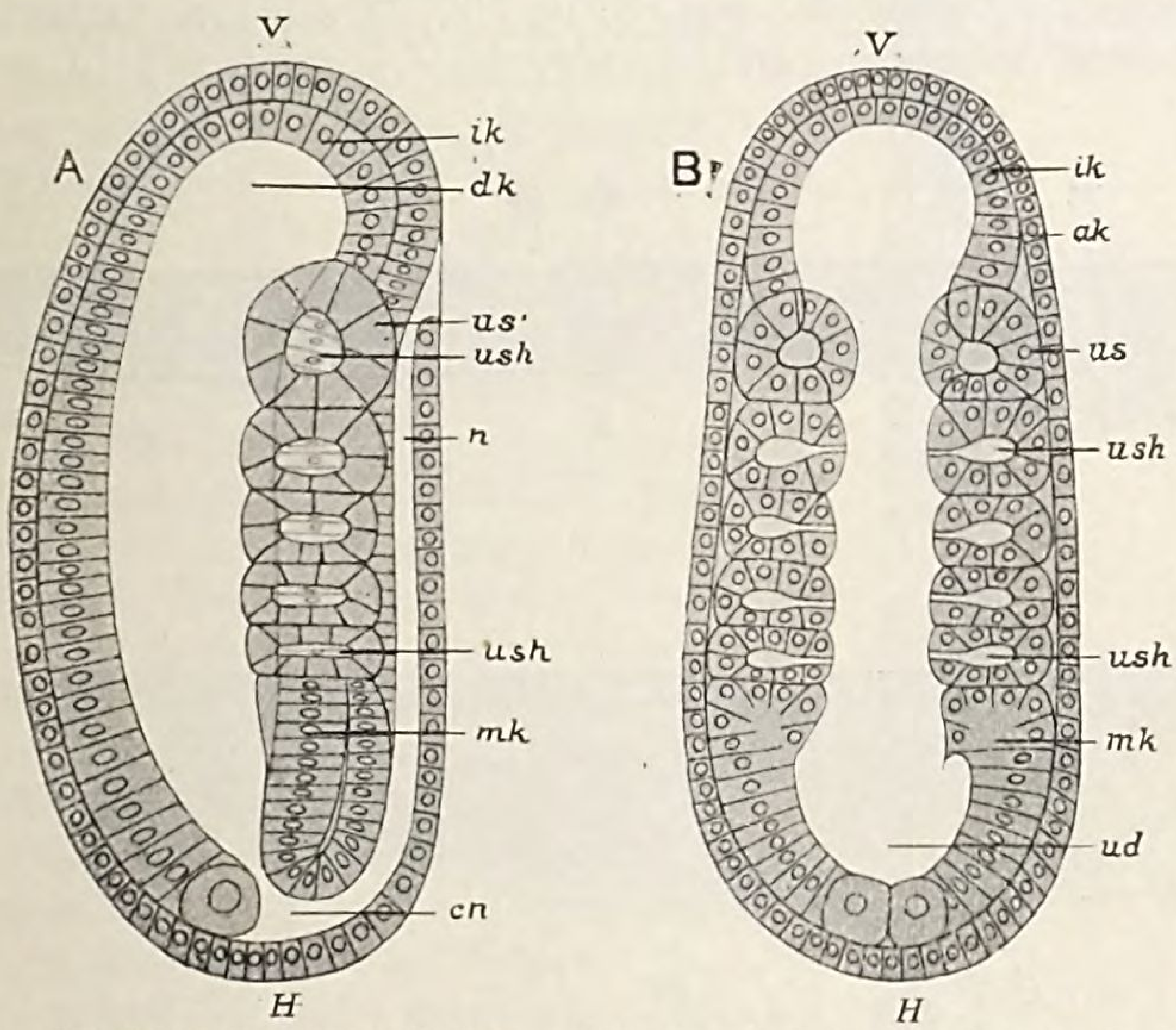


FIG. 707.—**Amphioxus lanceolatus.** Embryo. A, from the side; B, in horizontal section. *ak*, ectoderm; *cn*, neurenteric canal; *dh*, archenteron; *ik*, endoderm; *mk*, mesodermal folds; *n*, neural tube; *ud*, archenteron; *us*, first cœlomic pouch; *ush*, cœlomic cavity; *V*, anterior; *H*, posterior end. (From Korschelt and Heider, after Hatschek.)

end of the archenteron: its final extension to the end of the snout is a subsequent process.

New cœlomic pouches are formed in regular order from before backwards, the embryo at the same time elongating and becoming laterally compressed and pointed fore and aft. At the anterior end the *mouth* (Fig. 708, *m*) appears on the left side of the body as a small aperture, which soon increases greatly in size. On the ventral surface another small aperture, the *first gill-slit* (*ks*) makes its appearance, and soon shifts over to the right side: it forms a direct communication between the pharynx and the exterior, like the stigmata of Appendicularia (p. 21): there is at present no trace of the atrium.

The anterior end of the archenteron has meanwhile grown out

into a pair of pouches, which become shut off as closed sacs: of these the right gives rise to the cœlome of the head (h), the left to a depression called the *præ-oral pit* (w), from which the groove of Hatschek is afterwards formed. On the floor of the archenteron, in the neighbourhood of the mouth, a depression appears, which gives rise to a structure called the *club-shaped gland* (k). Posteriorly the neurenteric canal closes and the anus appears.

We left the mesoderm in the form of separate paired cœlomic sacs, arranged metamerically in the dorsal region of the embryo. The sacs increase in size, and extend both upwards and downwards, each presenting a *somatic layer* (Fig. 706, D, mk^1) in contact with the external ectoderm, and a *splanchnic layer* (mk^2) in contact

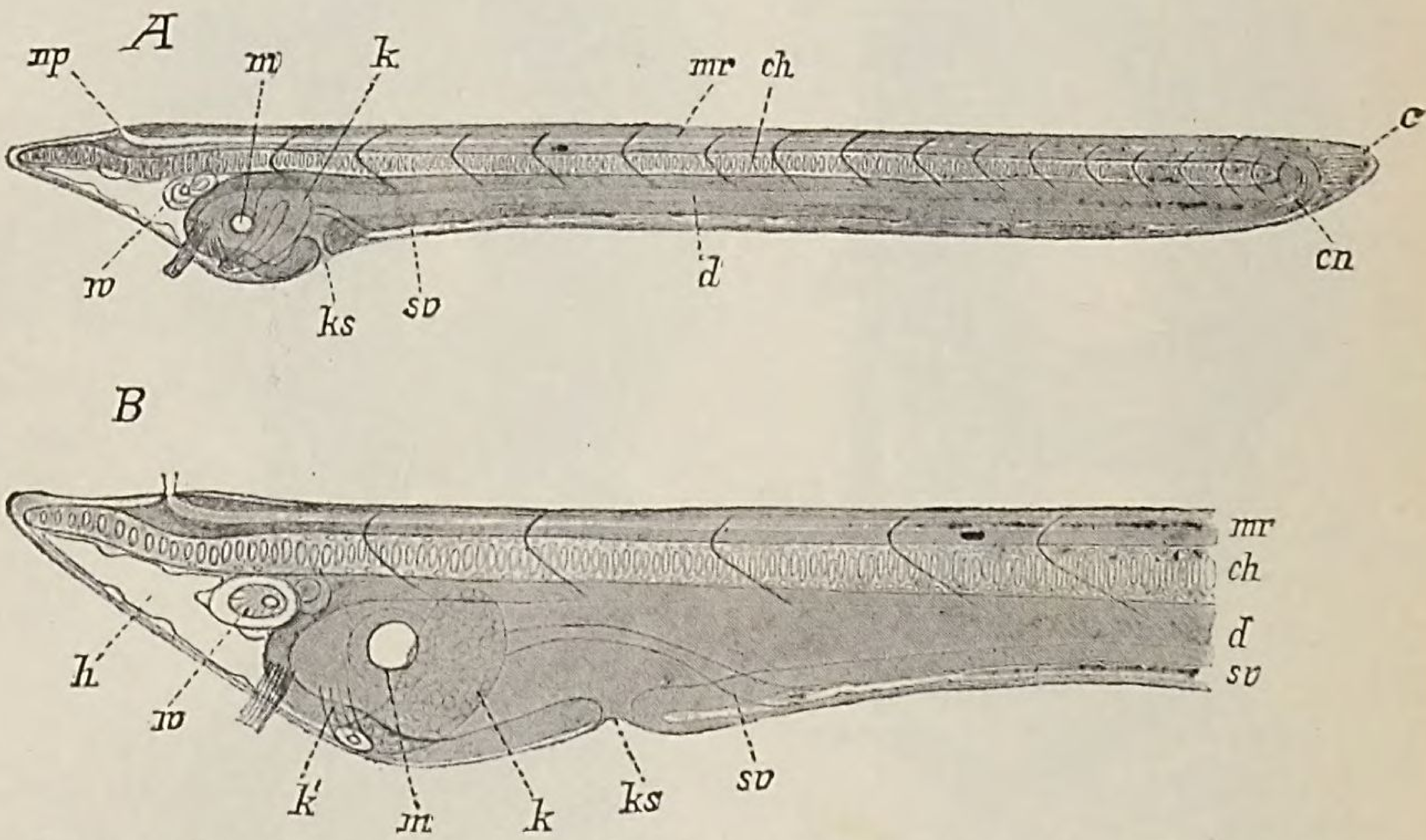


FIG. 708.—**Amphioxus lanceolatus.** A, young larva; B, anterior end more highly magnified. *c*, provisional tail-fin; *ch*, notochord; *cn*, neurenteric canal; *d*, enteric canal; *h*, cœlome of head; *k*, club-shaped gland; *k'*, its external aperture; *ks*, first gill-slit; *m*. mouth; *mr*. nerve-tube; *np*. neuropore; *sv*. sub-intestinal vein; *w*, præ-oral pit. (From Korschelt and Heider, after Hatschek.)

with the nervous system and notochord dorsally, and with the enteric canal ventrally. At about the level of the ventral surface of the notochord, a horizontal partition is formed in each cœlomic sac (Fig. 706, D), separating it into a dorsal and ventral portion. The dorsal section is distinguished as the *protovertebra* (ns), and its cavity as the *myocœle* or muscle-cavity: the ventral section is called the *lateral plate*, and its cavity forms a segment of the cœlome.

The ventral plates now unite with one another in pairs below the enteric canal, their cavities becoming continuous: at the same time the cavities of successive ventral plates are placed in communication with one another by the absorption of their

adjacent (anterior and posterior) walls. In this way the cavities of the entire series of ventral plates, right and left, unite to form the single unsegmented cœlome of the adult, their walls giving rise to the cœlomic epithelium.

At the same time the cells of the splanchnic layer of the protovertebræ become converted into muscular fibres, which nearly fill the myocœle, and give rise to the myomeres: the myocommas arise from the adjacent anterior and posterior walls of the protovertebræ. An outpushing of the splanchnic layer, at about the level of the ventral surface of the notochord, grows upwards between the myomere externally and the notochord and nerve-tube internally: from the cells lining this pouch the connective-tissue sheath of the notochord and nervous system arises, and perhaps also the fin-rays. From the parietal layer of the protovertebræ arises the derm or connective tissue layer of the skin.

The larva increases in size, and becomes very long and narrow, with a pointed anterior end and a provisional caudal fin posteriorly (Fig. 709, *c*). As growth proceeds, new segments are added behind those already formed, the notochord grows forwards to the anterior end of the snout, and the eye-spot (*au.*) and olfactory pit appear, the latter as an ectodermal pit which communicates with the neurocœle by the still open neuropore (*np.*). The mouth (*m.*) attains a relatively immense size, still remaining on the left side.

Additional gill-slits appear behind the one already mentioned: they all make their appearance near the middle ventral line, and gradually shift over to the right side: at first they correspond with the myomeres, so that the segmentation of the pharynx is part of the general metamerism of the body. Altogether fourteen clefts are

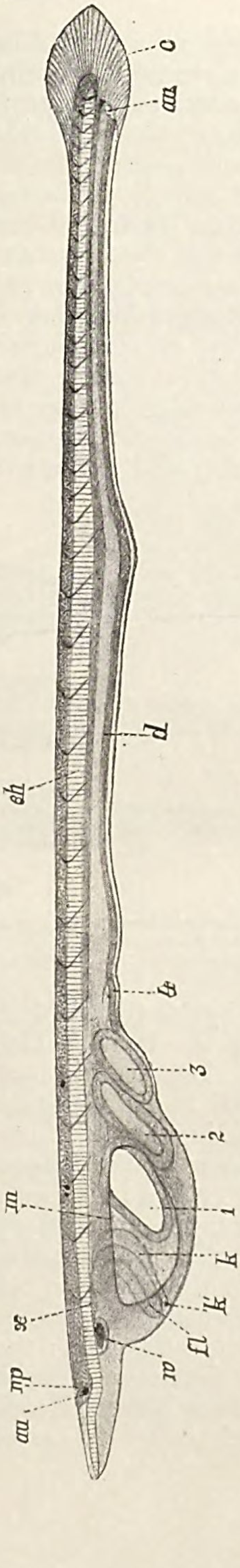


FIG. 709.—**Amphioxus lanceolatus.** More advanced larva. *an.* anus; *au*, eye-spot; *c*, larval tail-fin; *ch*, notochord; *d*, enteric canal; *fl*, rudiment of endostyle; *k*, club-shaped gland; *k'*, its external aperture; *m.* mouth; *np.* neuropore; *w*, præ-oral pit; *x*, provisional nephridium; *1–4*, gill-slits. (From Korschelt and Heider, after Lankester and Willey.)

produced in a single longitudinal series. Above, *i.e.* dorsal to them, a second longitudinal series makes its appearance, containing eight clefts, so that at this stage there are two parallel rows of gill-slits on the right side of the body, and none on the left. But as growth goes on, the first or ventral series gradually travels over to the left side, producing a symmetrical arrangement, and at the same time the first slit and the last five of the first or definitively left series close up and disappear, so that the numbers are equalised on the two sides. At first each gill-slit is simple, but before long a fold grows down from its dorsal edge, and, proceeding ventrally, divides the single aperture into two: this fold is the secondary or tongue lamella, the original bars of tissue between the undivided slits becoming the primary lamellæ.

While the development of the gill-slits is proceeding, the atrium is in course of formation. Paired longitudinal ridges, the *meta-*

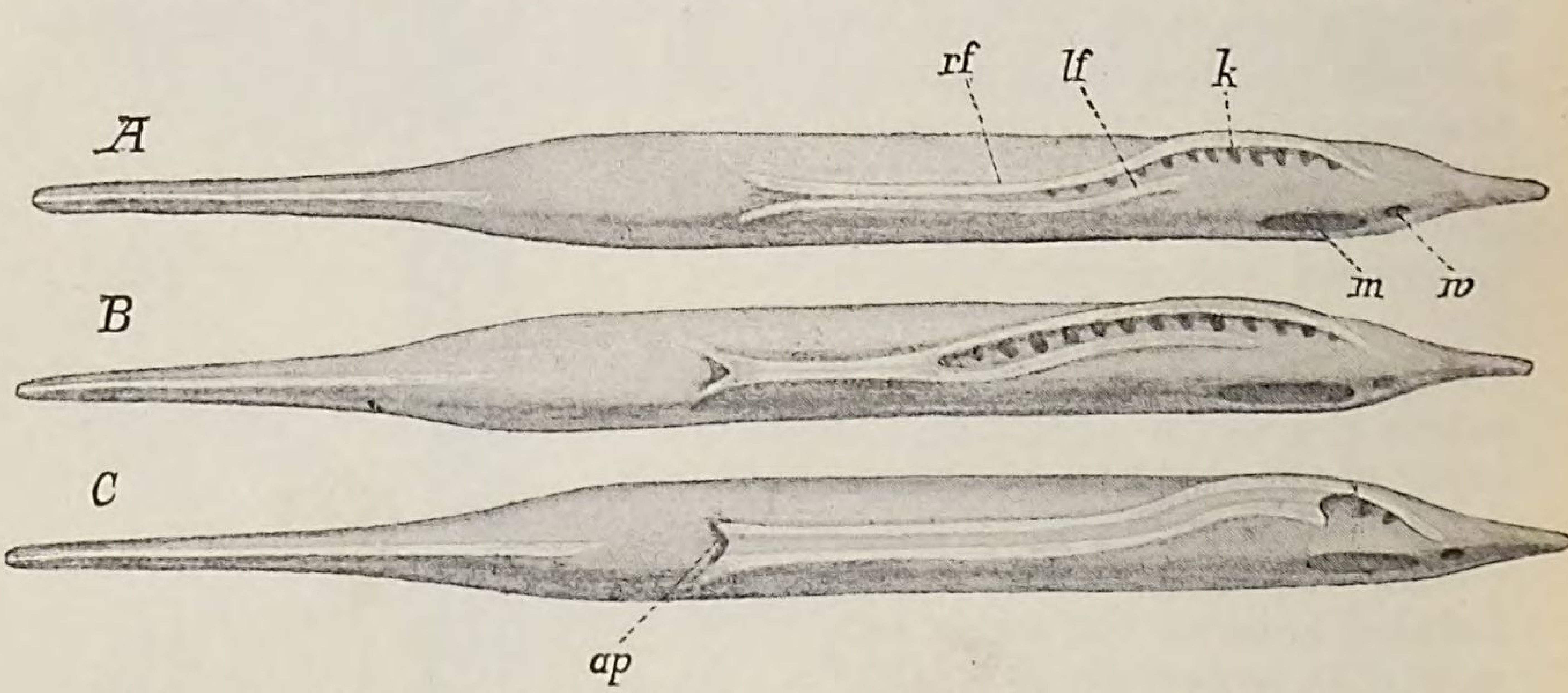


FIG. 710.—**Amphioxus lanceolatus.** Ventral aspect of three larvæ showing the development of the atrium. *ap.* atriopore ; *k*, gill-slits ; *lf.* left metapleural fold ; *m.* mouth ; *rf.* right metapleural fold ; *w*, præ-oral pit. (From Korschelt and Heider, after Lankester and Willey.)

pleural folds (Fig. 710, *lf. rf.*, Fig. 711, *sf.*) appear on the ventral side of the body, behind the gill-slits, and gradually extend forwards, dorsal to the latter, their arrangement being very unsymmetrical in correspondence with that of the clefts themselves. On the inner face of each fold, *i.e.* the face which looks towards its fellow of the opposite side, a longitudinal *sub-atrial ridge* (Fig. 711, A, *sl*) appears, and, the two sub-atrial ridges meeting and coalescing, a canal (B, *p*) is formed immediately below the ventral body-wall. This canal is the commencement of the atrium: it is at first quite narrow, but gradually extends upwards on each side (C, *p*) until it attains its full dimensions. It is open, at first, both in front and behind: the posterior opening remains as the atriopore: the anterior opening becomes gradually shifted forwards as the fusion of the sub-atrial ridges proceeds (Fig. 710, B and C), and is finally completely closed. In this way the gill-slits come to open,

not directly on the exterior, but into a cavity formed by the union of paired ridges of the body-wall, and therefore lined by ectoderm.

The mouth gradually passes to the ventral surface, and undergoes a relative diminution in size: a fold of integument develops round it, and forms the oral hood, which is probably to be looked upon as a stomodæum. The endostyle appears on the right of the pharynx (Fig. 709, *ft*), and is at first rod-shaped, then V-shaped: ultimately the limbs of the V unite in the middle ventral line. The gill-slits increase in number, and become more and more vertically elongated. The provisional caudal fin disappears. The gonads arise from the outer and ventral regions of the proto-

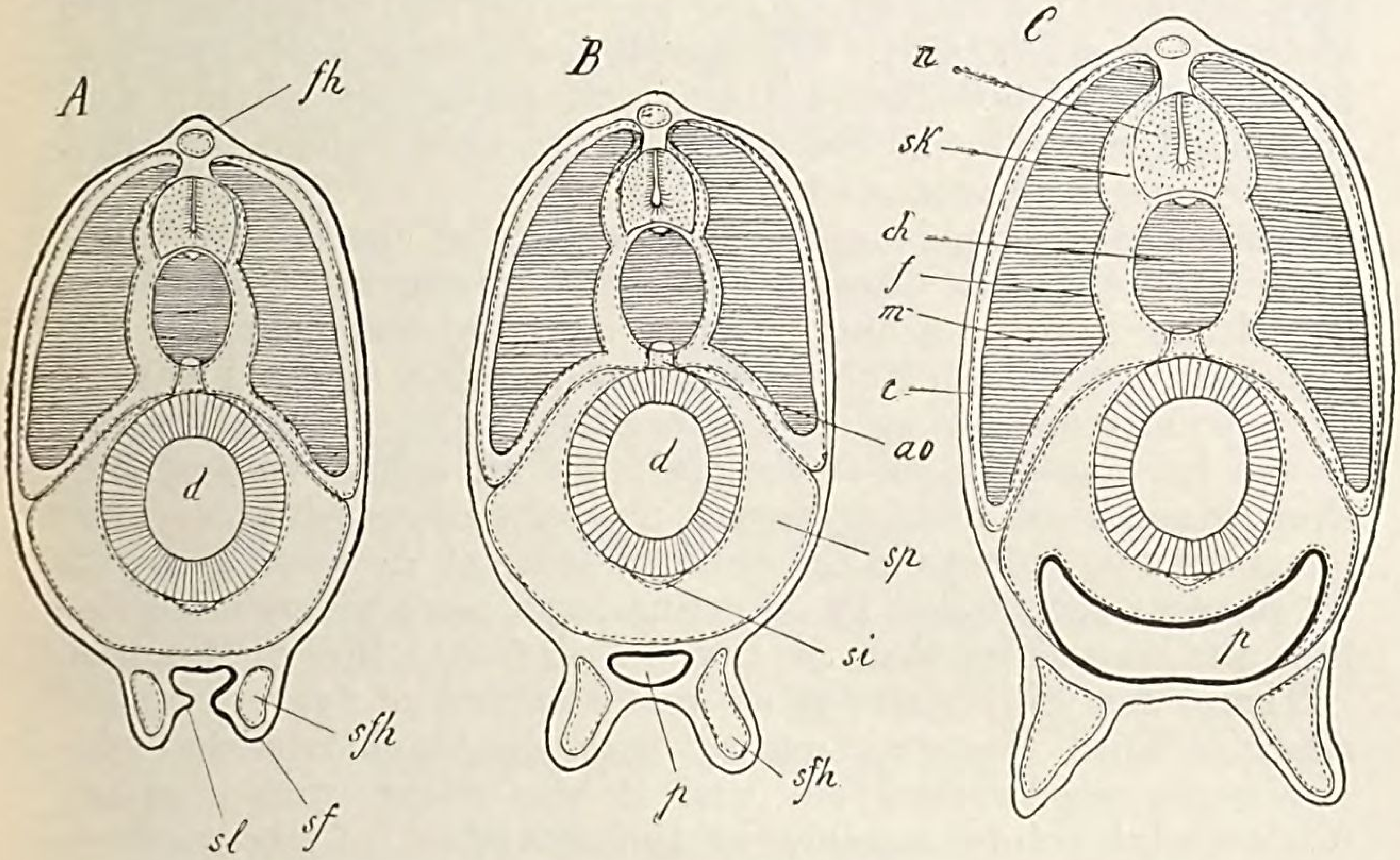


FIG. 711.—**Amphioxus lanceolatus.** Diagrammatic transverse sections of three larvæ to show the development of the atrium. *ao.* aorta; *c*, dermis; *d*, intestine; *f.* fascia; *fh*, cavity for dorsal fin-ray; *m.* myomere; *n.* nerve-tube; *p*, atrium; *sf.* metapleural folds; *si.* sub-intestinal vein; *sk*, sheath of notochord and neuron; *sl.* sub-atrial ridge; *sp.* cœlome. (From Korschelt and Heider, after Lankester and Willey.)

vertebræ in the form of pouches, which gradually assume their permanent form. The development of the nephridia is not known, but an organ, considered to be a provisional nephridium (Fig. 709, *x*), is formed in the mesoderm of the first metamere, and opens into the pharynx: it disappears in the adult.

Distribution.—Amphioxus has been found in the North Atlantic and Mediterranean, on the west coast of North America, the East Indies, the east coast of South America, Australia, New Zealand, and the Malayan Islands. Asymmetron was first known from the Bahamas, and a second closely allied species has been found in the Louisiade Archipelago. As might be expected, no fossil remains of the group are known.

Distinctive Characters.—The Acrania may be defined as Vertebrata in which the notochord extends to the anterior end of the snout, in advance of the central nervous system. There is no skull, and no trace of limbs. The ectoderm consists of a single layer of cells which may be ciliated. The pharynx is of immense size, perforated by very numerous gill-slits, and surrounded by an atrium. The liver is a hollow pouch of the intestine. There is no heart, and the blood is colourless. The nephridia remain distinct and open into the atrium. The brain is very imperfectly differentiated; there are only two pairs of cerebral nerves; and the dorsal and ventral spinal nerves do not unite. There are no paired eyes, but there is a median pigment spot in the wall of the brain; the auditory organ is absent. The gonads are metamerically arranged and have no ducts. There is a typical invaginate gastrula, and the mesoderm arises in the form of metameric cœlomic pouches. The cœlome is an enterocœle.

Affinities.—Amphioxus has had a somewhat chequered zoological history. Its first discoverer placed it among the Gastropoda, considering it to be a Slug. When its vertebrate character was made out, it was for a long time placed definitely among Fishes as the type of a distinct order of that class, but it became obvious, from a full consideration of the case, that an animal with neither skull, brain, heart, auditory organs, nor paired eyes, with colourless blood, with no kidneys in the ordinary sense of the word, and with its pharynx surrounded by an atrium, was more widely separated from the lowest Fish than the lowest Fish from a Bird or Mammal.

There was still, however, no real suspicion of "invertebrate" affinities until the development both of Amphioxus and the Urochorda was worked out, and it was shown that in many fundamental points, notably in the formation of the nervous system and the notochord, there was the closest resemblance between the two. The likeness was further emphasised by the presence in both forms of an endostyle, an epipharyngeal groove, and peripharyngeal bands, and of an atrium, and by the obvious homology of the gill-slits of Tunicates with those of Amphioxus. The Urochorda being obviously a degenerate group, it was suggested that the peculiarities of the adult Amphioxus might also be due to a retrogressive metamorphosis. Of this, however, there is no evidence, and all recent investigations and especially the discovery of the nephridia, have tended to bring the Acrania nearer to the Craniate Vertebrata, and to remove them urther from the lower Chordata.

DIVISION B.—CRANIATA.

The group of Craniate Vertebrata includes all those animals known as Fishes, Amphibians, Reptiles, Birds, and Mammals, or, in

other words, Vertebrata having a skull, a highly complex brain, a heart of three or four chambers, and red blood-corpuscles.

In spite of the obvious and striking diversity of organisation obtaining among Craniata, between, for instance, a Lamprey, a Pigeon, and a Dog, there is a fundamental unity of plan running through the whole group, both as to the general arrangement of the various systems of organs and the structure of the organs themselves, far greater than in any of the principal invertebrate groups. The range of variation in the whole of the six classes included in the division is, in fact, considerably less than in many single classes of Invertebrata, for instance, Hydrozoa or Crustacea. Hence, while the plan hitherto adopted of treating the group class by class will be followed, it will be found convenient to begin by devoting a considerable space to a preliminary account of the Craniata as a whole, since in this way much needless repetition will be avoided.

The Craniata include the following classes and sub-classes:—

CLASS I.—CYCLOSTOMATA,

Including the Lampreys and Hags.

CLASS II.—PISCES,

Including the true Fishes, which are again divisible into

Sub-class 1.—*Elasmobranchii*,

Including the Sharks and Rays.

Sub-class 2.—*Holocephali*,

Including only the Cat-fish (*Chimæra*) and the Elephant-fish (*Callorhynchus*).

Sub-class 3.—*Teleostomi*,

Including the bony Fishes, such as Perch, Cod, Trout, &c. and the Sturgeons and their allies.

Sub-Class 4.—*Dipnoi*,[1]

Including the Amphibious Fishes or Mud-fishes.

CLASS III.—AMPHIBIA,

Including Frogs, Toads, Newts, and Salamanders.

[1] The animals included in Classes I and II are all "Fishes" in the broad sense of the word

CLASS IV.—REPTILIA,

Including Lizards, Snakes, Crocodiles, Turtles, and Tortoises.

CLASS V.—AVES,

Including Birds.

CLASS VI.—MAMMALIA,

Including Hairy Quadrupeds, Seals, Whales, Bats, Monkeys, and Man.

External Characters.—The body of Craniata (Fig. 712) is bilaterally symmetrical, elongated in an antero-posterior direction, and usually more or less cylindrical. It is divisible into three regions: the *head*, which contains the brain, the chief sensory organs, and the mouth and pharynx; the *trunk*, to which the cœlome is confined, and which contains the principal digestive and circulatory as well as the excretory and reproductive organs; and the *tail*, or region situated posteriorly to the cœlome and anus, and containing no essential organs. Between the head and trunk there is frequently a narrow region or *neck*, into which the cœlome does not extend. In aquatic Vertebrates the tail is of great size, not marked off externally from the trunk, and is the chief organ of locomotion: in terrestrial forms it becomes greatly reduced in diameter, and has the appearance of a mere unpaired posterior appendage.

The *mouth* (*mth.*) is a transverse aperture placed at or near the anterior end of the head. Near it, sometimes dorsal, sometimes ventral in position, are the paired *nostrils* or *anterior nares* (*na.*)—or in Cyclostomata the single nostril—leading to the organs of smell. Farther back, on the sides of the head, are the large *paired eyes* (*e.*), and on the dorsal surface there is sometimes more or less indication of a vestigial *median* or *pineal sense organ* (*pn. e.*), which may take the form of an eye. Posterior to the paired eyes are the *auditory organs* (*au.*), the position of which is indicated in the higher forms by an *auditory aperture.*

On the sides of the head, behind the mouth, are a series of openings, the *gill-slits* or *external branchial apertures* (*e. br. a. 1—7*): they are never more than seven in number, and in air-breathing forms disappear more or less completely in the adult. In the higher Fishes a fold called the *operculum* (Fig. 726, *op.*) springs from the side of the head immediately in front of the first gill-slit and extends backwards, covering the branchial apertures.

On the ventral surface at the junction of the trunk and tail is the *anus* (*an.*). Distinct *urinary* and *genital apertures,* or a single

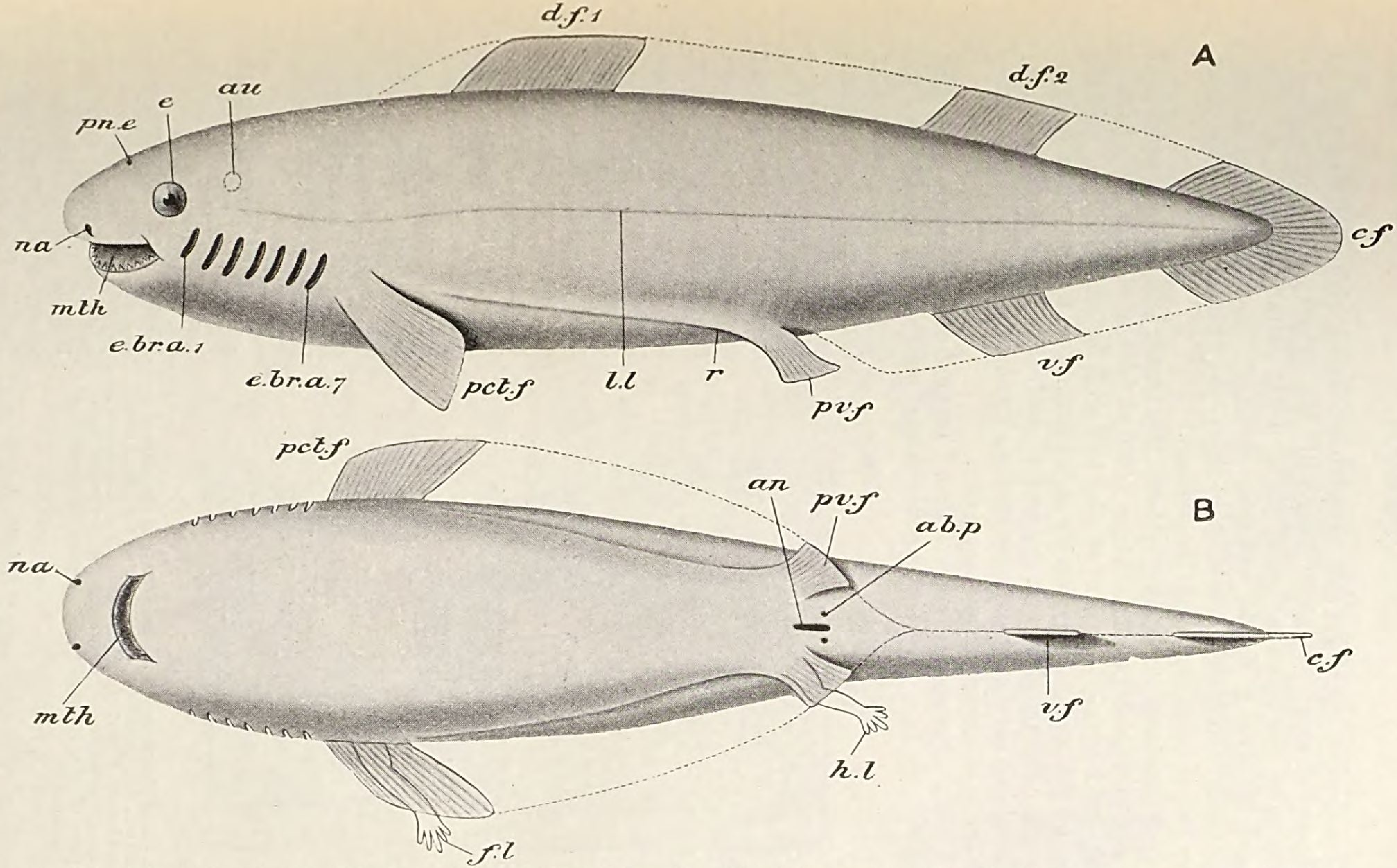


FIG. 712.—Lateral (A) and ventral (B) views of an ideal **Craniate.** *ab. p.* abdominal pore; *au.* position of auditory organ; *an.* anus; *c. f.* caudal fin; *d. f. 1,* first; *d. f. 2,* second dorsal fin; *e.* paired eye; *e. br. 1,* first; *e. br. 7,* seventh gill-cleft; *f. l,* fore-limbs; *l. l.* lateral line; *mth.* mouth; *na.* nasal aperture; *pct. f.* pectoral fin; *pn. e.* pineal sense organ; *pv. f.* pelvic fin; *r.* pre-pelvic ridge; *v. f,* ventral line. The dotted lines indicate continuous median and paired fins.

urino-genital aperture, are sometimes found either in front of or behind the anus, but more commonly the urinary and genital ducts open into the termination of the enteric canal, or *cloaca*, so that there is only a single egestive opening, known as the *cloacal aperture*. On either side of this there may be a small *abdominal pore* (*ab. p.*) leading into the cœlome.

In Fishes and some Amphibians, the trunk and tail are produced in the middle dorsal line into a vertical fold or *median fin*, which is continued round the end of the tail and forwards in the middle line to the anus. Frequently this continuous fin becomes broken up into distinct *dorsal* (*d. f. 1* and *2*), *ventral* (*v. f.*), and *caudal* (*c. f.*) *fins*, which may assume very various forms: in the higher classes all trace of median fins disappears.

Fishes also possess *paired fins*. Immediately posterior to the last gill-slit is a more or less horizontal outgrowth, the *pectoral fin* (*pct. f.*), while a similar but smaller structure, the *pelvic fin* (*pv. f.*), arises at the side of the anus. In the embryonic condition there is sometimes found to be a low ridge (*r.*) connecting the pectoral and pelvic fins of each side with one another, and from this and other considerations there is reason for thinking that the paired fins are detached and enlarged portions of a continuous *lateral fin*, having similar anatomical relations to the metapleural folds of Amphioxus.

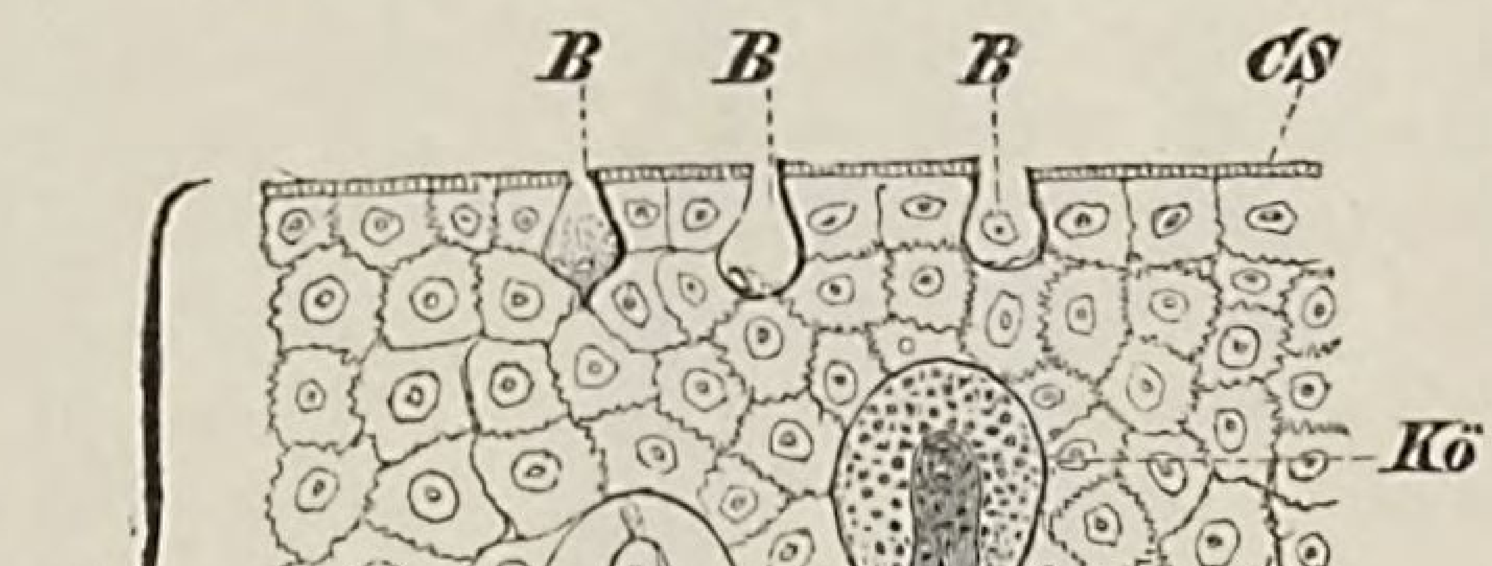


FIG. 713.—Diagrammatic vertical section of the skin of a **Fish.** *B*, unicellular mucous glands; *Co*, derm; *Ep.* epiderm; *F.* fat; *G*, blood-vessels; *Ko*, goblet-cells; *Kö*, granule-cells; *S*, vertical, and *W*, horizontal bundles of connective tissue. (From Wiedersheim's *Vertebrata*.)

In all Craniata above Fishes, *i.e.*, from Amphibia upwards, the paired fins are replaced by *fore-* and *hind-limbs* (*f.l.*, *h.l.*), each consisting of three divisions—*upper-arm*, *fore-arm*, and *hand* in the one case; *thigh*, *shank*, and *foot* in the other. Both hand and foot normally terminate in five fingers or *digits*, and the *pentadactyle limb* thus formed is very characteristic of all the

higher Vertebrata. The paired fins or limbs, as the case may be, are the only lateral appendages possessed by Vertebrates.

Body-wall and Internal Cavities.—The body is covered externally by a *skin* consisting of two layers, an outer or epithelial layer, the *epidermis* (Fig. 713, *Ep.*), derived from the ectoderm of the embryo, and an inner or connective-tissue layer, the *dermis* (*Co*), of mesodermal origin. The epidermis is always many-layered, the cells of the lower layers, forming the *stratum Malpighii*, being protoplasmic and capable of active multiplication, while those of the superficial layers often become flattened and horny, and constitute the *stratum corneum*. *Glands* are often present in the skin in the form of tubular or flask-shaped in-pushings of the epidermis or of isolated gland-cells (B).

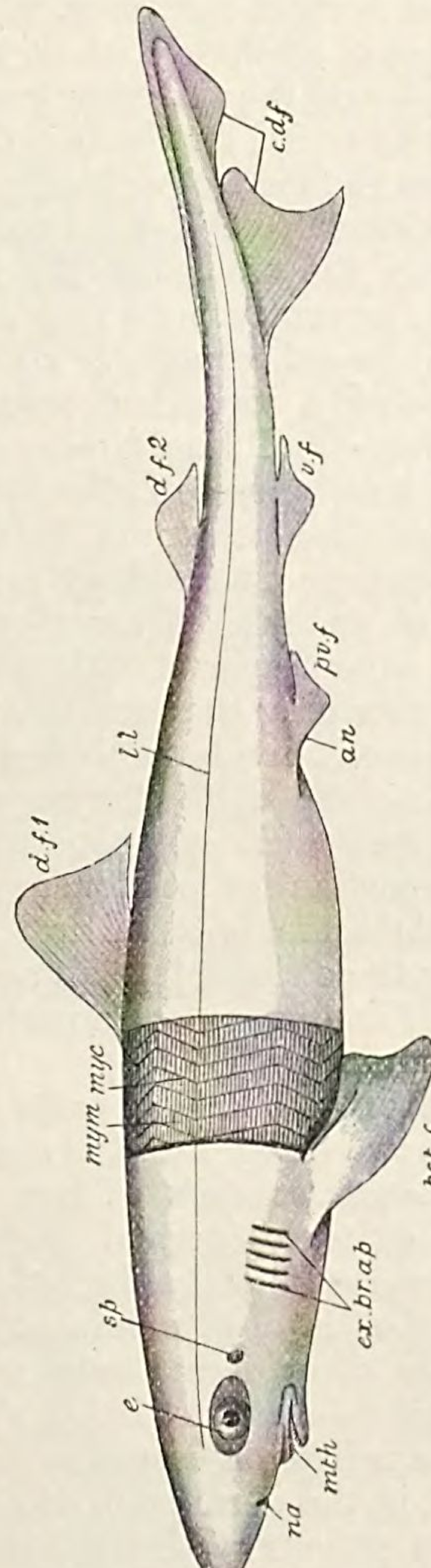


Fig. 714.—Side view of **Dogfish** (*Mustelus antarcticus*), with a strip of skin in the middle of the body removed to show the muscles. *an.* anus; *cd. f.* caudal fin; *d. f. 1, d. f. 2,* dorsal fins; *e.* eye; *ext. br. ap.* external branchial apertures; *l. l.* lateral line; *mth.* mouth; *myc.* myocommas; *mym.* myomeres; *n. a.* nasal aperture; *pct. f.* pectoral fin; *pv. f.* pelvic fin; *sp.* spiracle; *v. f.* ventral fin. (From Parker's *Biology*.)

Beneath the skin comes the *muscular layer*. This is always highly developed, and, in the lower Craniata, has the same general arrangement as in Amphioxus, *i.e.* consists of zig-zag muscle-segments or *myomeres* (Fig. 714, *mym.*), separated from one another by partitions of connective tissue, or *myocommas* (*myc.*), and formed of longitudinally disposed muscle-fibres. The myomeres are not placed at right angles to the long axis of the body, but are directed from the sagittal plane outwards and backwards, and are at the same time convex in front and concave behind, so as to have a cone-in-cone arrangement (Fig. 715, C). Each myomere, moreover, is divisible into a dorsal (*d. m.*) and a ventral (*v. m.*) portion. In the higher groups this segmental arrangement, though present in the embryo, is lost in the adult, the myomeres becoming converted into more or less longitudinal bands, having an extremely complex arrangement.

In the trunk, as shown by a section of that region, the muscles form a definite layer beneath the skin and enclosing the *cœlome* (Fig. 715, A and C, *cœl.*). The muscular layer, as in Amphioxus, is not of even diameter throughout, but is greatly thickened dorsally, so that the cœlome is, as it were, thrown towards the ventral side. Its dorsal portion, moreover, is excavated by a canal, the *neural* or *cerebro-spinal cavity* (*c. s. c.*), in which the central nervous system is contained, and the anterior portion of which is always dilated, as the *cranial cavity*, for the brain. Thus a transverse section of the trunk has the form of a double tube. In the head, neck, and tail, (B, D), the cœlome is absent in the adult, and the muscles occupy practically the whole of the interval between the skin and the skeleton, presently to be referred to: in the tail, however, there is found a *hæmal canal* (*h. c.*) containing connective tissue, and representing a virtual backward extension of the cœlome. The fins, or fore- and hind-limbs, are moved by longitudinal muscles derived from those of the trunk. All the voluntary or body-muscles of Craniata are of the striped kind.

The cœlome is lined by *peritoneum* (C, *pr.*), a membrane consisting of an outer layer of connective tissue, next the muscles, and an inner layer of cœlomic epithelium bounding the cavity, and thus forming the innermost layer of the body-wall. In Fishes the cœlome is divided into two chambers, a large *abdominal cavity* containing the chief viscera, and a small forwardly-placed *pericardial cavity* (A. *pc.*) containing the heart, and lined by a detached portion of peritoneum known as the *pericardium*. In Mammals there is a vertical muscular partition, the *diaphragm*, dividing the cœlome into an anterior chamber or *thorax*, containing the heart and lungs, and a posterior chamber or *abdomen* containing the remaining viscera.

Skeleton.—The hard parts or supporting structures of Craniata fall into two categories, the *exoskeleton* and the *endoskeleton*. The **exoskeleton** consists of bony or horny deposits in the skin, and may be either epidermal or dermal, but is never, like the armour of an Arthropod or the shell of a Mollusc, cuticular. The epidermal exoskeleton is always formed by the cornification or conversion into horn of epidermal cells, and may take the form of scales—as in Reptiles—feathers, hairs, claws, nails, horns, and hoofs. The dermal exoskeleton occurs in the form of either bony or horn-like deposits in the derm, such as the scales and fin-rays of Fishes, and the bony armour of the Sturgeon, Crocodile, or Armadillo. Some recent researches tend to show that the dermal exoskeleton may be ectodermal and not mesodermal in its ultimate origin.

The **endoskeleton**, or "skeleton" in the ordinary sense of the word, forms one of the most complex portions of the body, and presents an immense range of variation in the different classes and orders. As in Amphioxus, the axis of the entire skeletal system

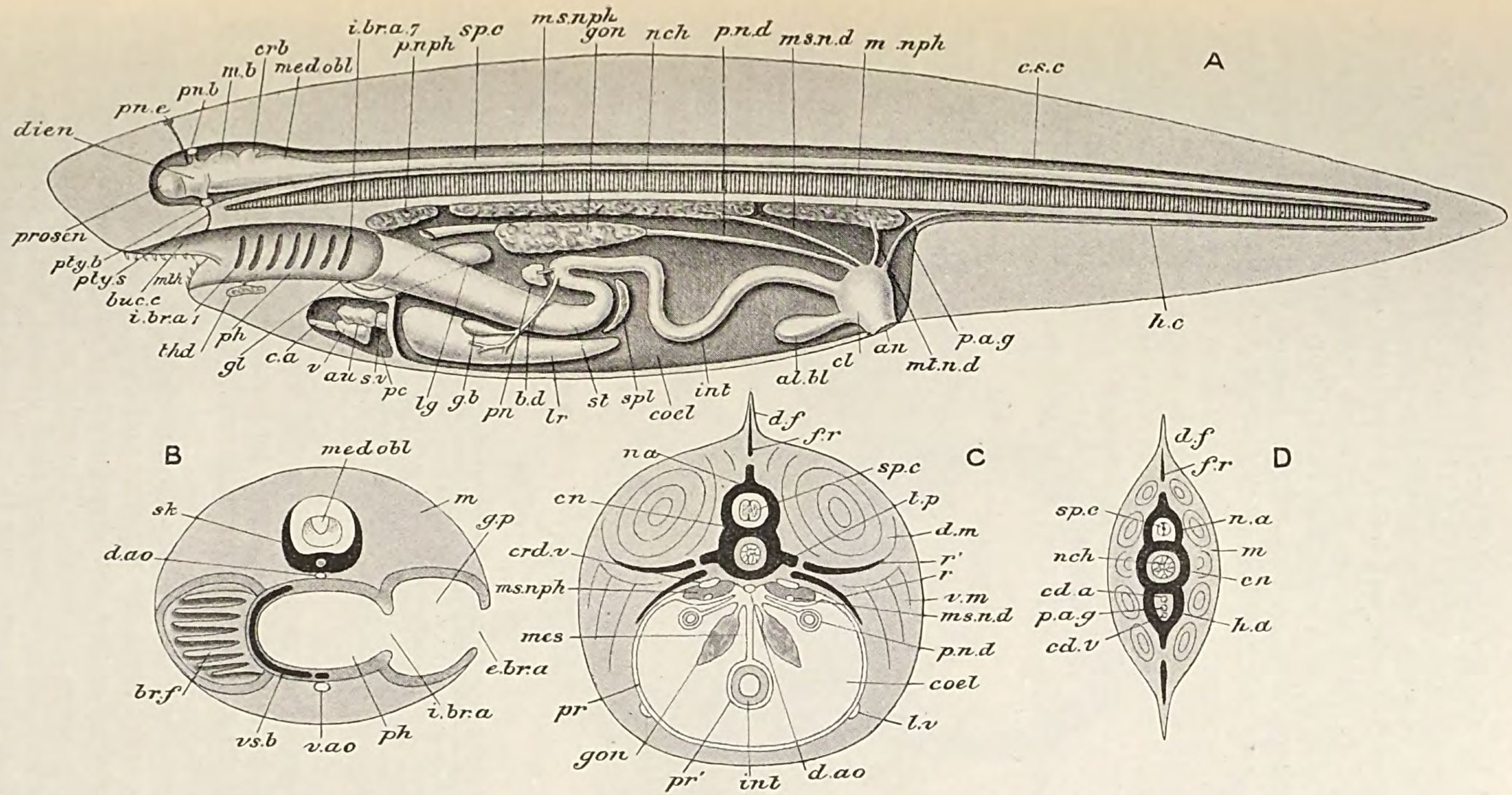


FIG. 715.—A, sagittal section of ideal **Craniate**; B, transverse section of the head; C, of the trunk; D of the tail. *al. bl.* allantoic bladder; *an.* anus; *au.* auricle; *b. d.* bile-duct; *br. f.* branchial filaments; *buc. c.* buccal cavity; *c. a.* conus arteriosus; *cd. a.* caudal artery; *cd. v.* caudal vein; *cœl.* cœlome; *crd. v.* cardinal vein; *cn.* centrum; *crb.* cerebellum; *c. s. c.* cerebro-spinal cavity; *d. ao.* dorsal aorta; *dien.* diencephalon; *d. f.* dorsal fin; *d. m.* dorsal muscles; *e. br. a.* external branchial aperture; *f. r.* fin-ray; *g. b.* gall-bladder; *gl.* glottis; *gon.* gonad; *g. p.* gill-pouch; *h. a.* hæmal arch; *h. c.* hæmal canal; *i. br. a.* internal branchial apertures; *int.* intestine; *lg.* lung; *lr.* liver; *l. v.* lateral vein; *m.* muscles; *m. b.* mid-brain; *med. obl.* medulla oblongata; *mes.* mesentery; *ms. n. d.* mesonephric duct; *ms. nph.* mesonephros; *mth.* mouth; *mt. n. d.* metanephric duct; *mt. nph.* metanephros; *n. a.* neural arch; *nch.* notochord; *p. a. g.* post-anal gut; *pc.* pericardium; *ph.* pharynx; *pn.* pancreas; *pn. b.* pineal body; *p. n. d.* pronephric duct; *pn. e.* pineal sense-organ; *p. nph.* pronephros; *pr.* peritoneum, parietal layer; *pr'*, visceral layer; *prosen.* prosencephalon; *pty. b.* pituitary body; *pty. s.* pituitary sac; *r.* sub-peritoneal rib; *r'.* intermuscular rib; *sk.* skull; *sp. c.* spinal cord; *spl* spleen; *st.* stomach; *s. v.* sinus venosus; *thd.* thyroid; *t. p.* transverse process *v.* ventricle; *v. ao.* ventral aorta *v. m.* ventral muscles; *vs. b.* visceral bar.

is formed by the *notochord* (Fig. 715, *nch.*), an elastic rod made of peculiar vacuolated cells (Fig. 716, *nch.*), resembling the pith of plants, and covered by a laminated *sheath* (*sh. nch.*), with an *external elastic membrane* (*el. m.*) around it. The whole sheath is a cuticular product of the superficial notochordal cells (*nch. c.*), *i.e.*, is developed as a secretion from their outer or free surfaces. The notochord lies in the middle line of the dorsal body-wall between the cerebro-spinal cavity above and the cœlome below: it is usually developed, as in the lower Chordata, from a median longitudinal outgrowth of the dorsal wall of the gut. Posteriorly it extends to the end of the tail, but in front it always stops short of the anterior end of the head, ending near the middle of the brain immediately behind a peculiar organ, the *pituitary body* (Fig. 715, A, *pty.b.*), which will be referred to again in treating of the digestive organs and of the nervous system. The extension of the nervous system in front of the notochord is one of the most striking differences between the Craniata and Amphioxus, in which it will be remembered the notochord is prolonged to a considerable distance beyond the anterior end of the nerve-tube.

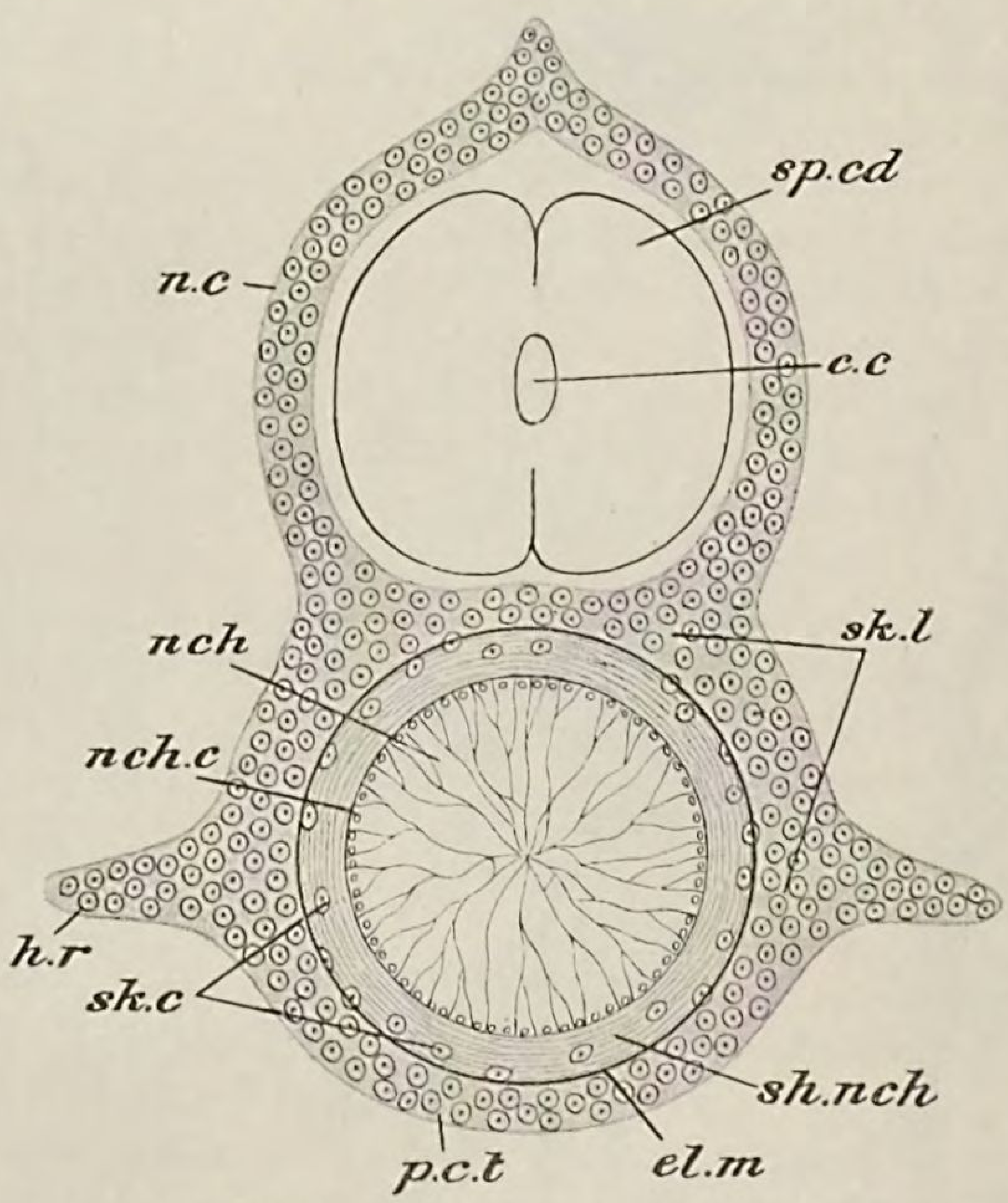


FIG. 716.—Semi-diagrammatic transverse section of the vertebral column of a **craniate embryo**; *c. c.* central canal; *el. m.* external elastic membrane; *h. r.* hæmal ridges; *n. c.* neural tube; *nch.* notochord; *nch. c.* notochordal cells; *p. c. t.* perichordal tube; *sh. nch.* sheath of notochord; *sk. c.* skeletogenous cells migrating into notochordal sheath; *sk. l.* skeletogenous layer; *sp. cd.* spinal cord. (Modified from Balfour and Gadow.)

In the majority of Craniata the notochord is a purely embryonic structure, and all but the anterior end of it is replaced in the adult by the *vertebral column*, the structure to which the entire vertebrate sub-phylum owes its name. The cells of mesoderm surrounding the notochord become concentrated around the sheath and give rise to the *skeletogenous layer* (Fig. 716, *sk. l.*), some of the cells of

which (*sk. c.*) may migrate into the sheath itself. In this way the notochord becomes surrounded by a cellular investment which soon takes on the structure of cartilage, and may be called the *perichordal tube* (Fig. 716, *p.c.t.*, and Fig. 717, *c.n.t.*). The skeletogenous layer also grows upwards and outwards, and gives rise to an inverted tunnel of cartilage, the *neural tube* (*n.c.*, *n.t.*), enclosing the cerebro-spinal cavity and connected below with the perichordal tube; and paired *hæmal ridges* (*h.r.*) of cartilage standing out from the sides of the perichordal tube into the muscles: in the region of the tail these unite below to enclose the *hæmal canal* (*h.t.*) already referred to. Actually, however, the vertebral column thus constituted is from the first more or less broken up into segments, and in the higher forms is replaced by a chain of bones called *vertebræ* which follow one another from before

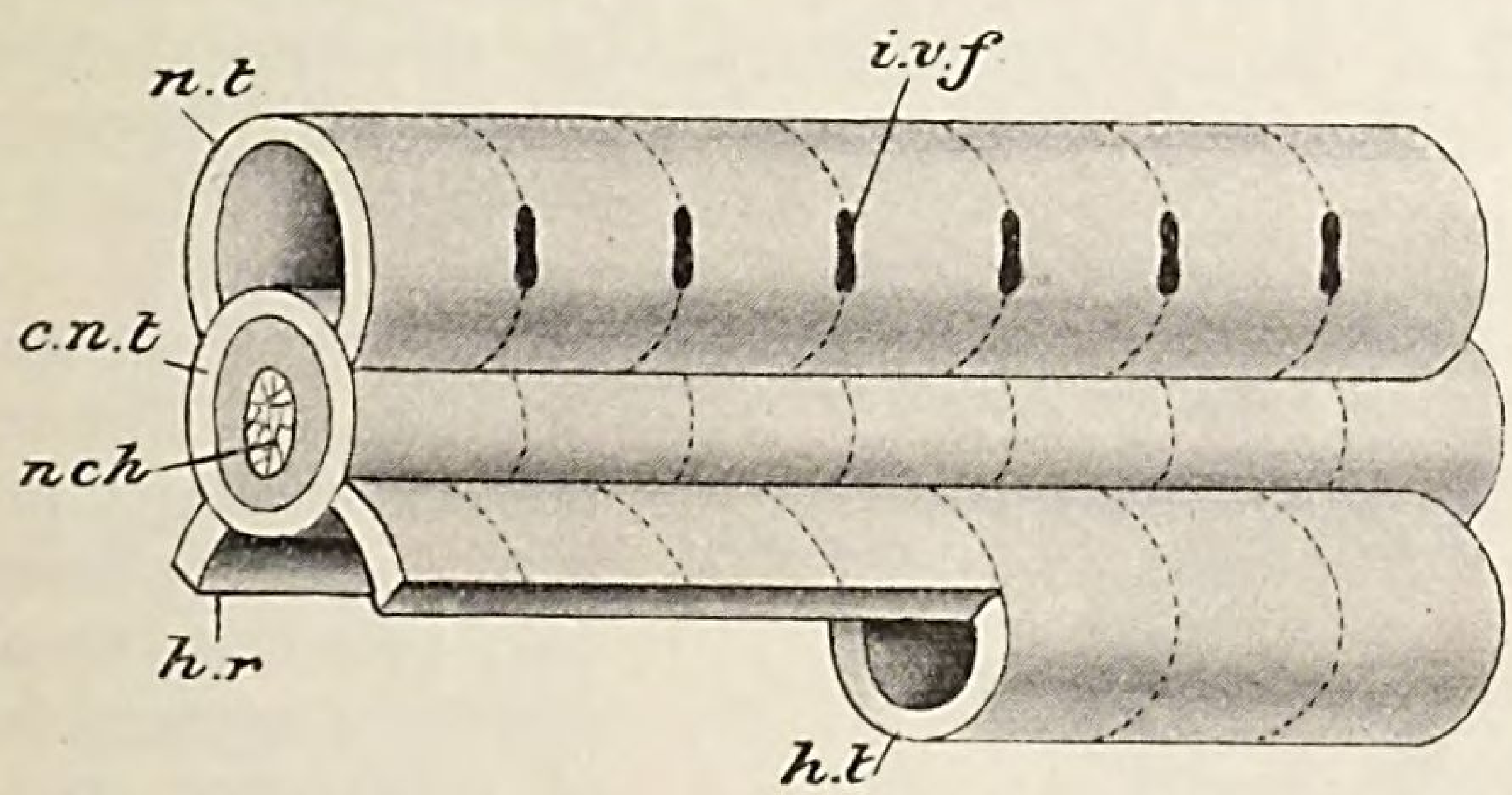


FIG. 717.—Diagram illustrating the segmentation of the vertebral column. *c. n. t.* perichordal tube; *h. r.* hæmal ridge; *h. t.* hæmal tube; *i. v. f.* inter-vertebral foramen; *n. t.* neural tube; *nch.* notochord. The dotted lines indicate the segmentation into vertebræ.

backwards, beginning a short distance behind the anterior end of the notochord and extending to the extremity of the tail.

A vertebra consists essentially of the following parts: (1) a *centrum* or *body* (Fig. 715, C, *cn.*) lying below the spinal canal in the position formerly occupied by the notochord and perichordal tube, and arising either in the skeletogenous layer proper, or in the notochordal sheath after its invasion by skeletogenous cells; (2) a *neural arch* (*n. a.*) which springs from the dorsal surface of the centrum and encircles the spinal canal, representing a segment of the neural tube; and (3) a pair of *transverse processes* (*t. p.*) which extend outwards from the centrum among the muscles and represent segments of the hæmal ridges: to them are often attached *ribs* which extend downwards in the body-wall, sometimes between the dorsal and ventral muscles (r^1), sometimes immediately external to the peritoneum (*r*). In the anterior part of the ventral body-wall a cartilaginous or bony *sternum* or breast-bone may be developed: in the Amphibia it is an independent structure; in the higher classes it is formed by the fusion of some

of the anterior ribs in the middle ventral line. In this way the anterior or thoracic region of the cœlome is enclosed in an articulated bony framework formed of the vertebral column above, the ribs at the sides, and the sternum below. The ribs under these circumstances become segmented each into two parts, a dorsal *vertebral rib,* articulating with a vertebra, and a ventral *sternal rib* with the sternum. In the tail there is frequently a *hæmal arch* (Fig. 715, D, *h. a.*) springing from the ventral aspect of the centrum and enclosing the hæmal canal. Thus the line of centra in the fully formed vertebral column occupies the precise position of the notochord; the neural arches encircle the spinal portion of the cerebro-spinal cavity; the transverse processes, ribs, and sternum encircle the cœlome; and the hæmal arches similarly surround the hæmal canal or vestigial cœlome of the tail. As we ascend the series of Craniata we find every gradation from the persistent notochord of the Cyclostomata, through the imperfectly differentiated vertebræ of Sharks and Rays, to the complete bony vertebral column of the higher forms.

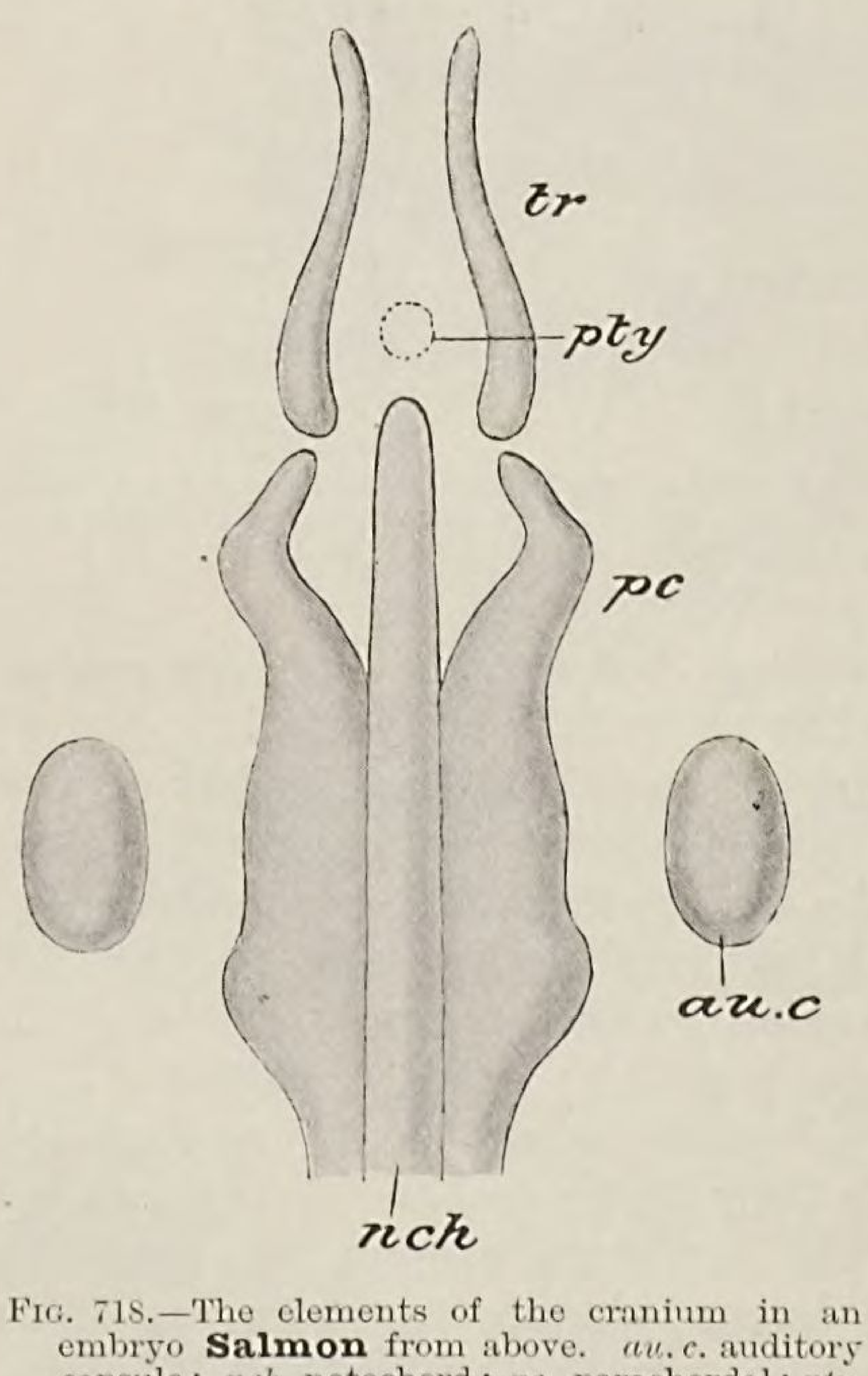


FIG. 718.—The elements of the cranium in an embryo **Salmon** from above. *au. c.* auditory capsule; *nch.* notochord; *pc.* parachordal; *pty.* position of pituitary body; *tr.* trabecula. (From a model by Ziegler.)

The vertebræ are equal in number to the myomeres, but are arranged alternately with them, the fibrous partition between two myomeres abutting against the middle of a vertebra, so that each muscle-segment acts upon two adjacent vertebræ. Thus, the myomeres being metameric or segmental structures, the vertebræ are intersegmental.

In connection with the anterior end of the notochord, where no vertebræ are formed, there are developed certain elements of the *skull* or cephalic skeleton, a structure eminently characteristic of the whole craniate division, and to the possession of which, indeed, it owes its name. The skull makes its first appearance in the embryo in the form of paired cartilaginous plates, the *parachordals* (Fig. 718, *pc*), lying one on each side of the anterior end of the notochord (*nch*) and thus continuing forward the line of vertebral

centra. In front of the parachordals are developed a pair of curved cartilaginous rods, the *trabeculæ* (*tr*), which underlie the anterior part of the brain, as the parachordals underlie its posterior part: their hinder ends diverge so as to embrace the pituitary body (*pty*) already referred to. Cartilaginous investments are also formed around the organs of the three higher senses: a pair of *olfactory capsules* round the organs of smell, one of *optic capsules* round the organs of sight, and one of *auditory capsules* (*au. c.*) round the organs of hearing. The optic capsule, which may be either fibrous, or cartilaginous, remains free from the remaining elements of the skull in accordance with the mobility of the eye; it constitutes, in fact, the *sclerotic* or outer coat of that organ. The olfactory capsules are usually formed as outgrowths of the trabeculæ, and are therefore continuous with those structures from the first. The auditory capsules are in some cases formed as outgrowths of the parachordals, in others arise as independent cartilages, each of which, however, soon unites with the parachordal of its own side. As development goes on, the trabeculæ and parachordals become fused into a single *basal plate* (Fig. 719, B, *b. cr.*) underlying the brain: the skull-floor thus formed gives off vertical up-growths on each side which finally close in above to a greater or less extent, and so give rise to a more or less complete *cranium* or brain-case enclosing the brain and the organs of smell and hearing, and furnishing open cavities or *orbits* for the eyes.

In the continuous solid cranial box thus formed certain definite regions are to be distinguished: a posterior or *occipital region*, formed from the parachordals, united or articulated with the anterior end of the vertebral column, and presenting a large aperture, the *foramen magnum* (Fig. 719, B, *for. mag.*), through which the spinal cord becomes continuous with the brain; an *auditory region* formed by the two outstanding auditory capsules (*au. cp.*); and a *trabecular region*, including all the rest. The latter is again divisible into an *inter-orbital region*, between the orbits or eye-sockets; an *olfactory region*, constituted by the olfactory capsules (A, *olf. cp.*), and by a median vertical plate, the *mesethmoid* (B. *ms. eth.*), which separates them from one another; and a *prenasal region* or *rostrum* (*r*) extending forwards from the mesethmoid and forming a more or less well-marked anterior prolongation of the cranium. The cavity for the brain (B) extends from the foramen magnum behind to the olfactory region in front; its floor, formed from the basal plate of the embryo, is called the *basis cranii* (*b. cr.*): its roof is always incomplete, there being one or more apertures or *fontanelles* (*fon.*) closed only by membrane and due to the imperfect union above of the side-walls.

In the walls of the brain-case are apertures or *foramina* for the passage outwards of the cerebral nerves (*vide infra*). The most important of these are the *olfactory foramina* (*nv.* 1) for the

nerves of smell, situated at the anterior end of the cerebral cavity, one on each side of the mesethmoid; the *optic foramina* (*nv.* 2) for the nerves of sight, in the interorbital region; the *trigeminal foramina* (*nv.* 5) for the fifth nerves, just in front of the auditory capsule; the *auditory foramina* (*nv.* 8) for the nerves of hearing, in the inner wall of the auditory capsules; and the *vagus foramina* (*Nv.* 10); for the tenth nerves, immediately posterior to the auditory capsules.

In addition to the elements of the brain-case—parachordals, trabeculæ, and auditory capsules—there enter into the composition

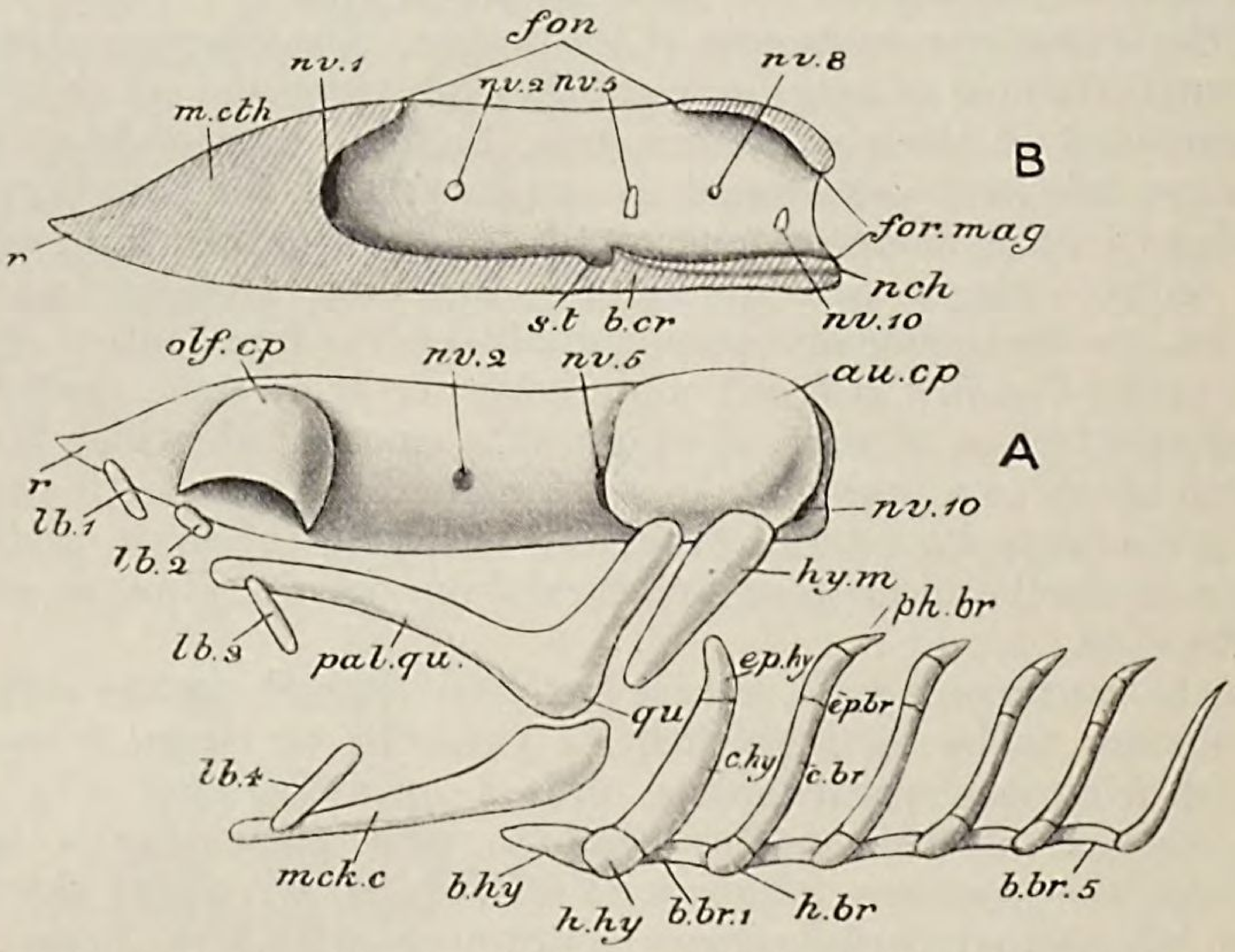


FIG. 719.—A, diagram of cartilaginous skull; B, cranium in sagittal section. *au. cp.* auditory capsule; *b. br. 1—5*, basi-branchials; *b. cr.* basis cranii; *b. hy.* basi-hyal; *c. br.* cerato-branchial; *c. hy.* cerato-hyal; *ep. br.* epi-branchial; *ep. hy.* epi-hyal; *fon.* fontanelle; *for. mag.* foramen magnum; *h. br.* hypo-branchial; *h. hy.* hypo-hyal; *hy. m.* hyomandibular; *lb. 1—4*, labial cartilages; *mck. c.* Meckel's cartilage; *m. eth.* mesethmoid; *nv. 1—10*, foramina for cerebral nerves; *olf. cp.* olfactory capsule; *pal. qu.* palato-quadrate; *ph. br.* pharyngo-branchial; *r.* rostrum; *s. t.* pituitary fossa or sella turcica.

of the skull another set of elements called *visceral bars*. These are cartilaginous rods formed in the walls of the pharynx between the gill-slits, and thus encircling the pharynx like a series of paired half-hoops (Fig. 715, B, *vs. b.*). The corresponding right and left bars become united with one another below by an unpaired cartilage (Fig. 719, A, *b. br.*), forming a *visceral arch*, and the unpaired ventral pieces unite successive arches with one another in the middle ventral line, thus giving rise to a more or less basket-like *visceral skeleton*. It will be noticed that the visceral skeleton has a segmental arrangement, being formed of parts arranged in an antero-posterior series, whereas in the cranium there is no indication whatever of segmentation. There is, however, no exact correspondence between

the segments of the visceral skeleton and the metameres. The visceral arches vary in number from four to nine: the foremost of them is distinguished as the *mandibular arch* and lies just behind the mouth; the second is called the *hyoid arch*, and the rest *branchial arches*, from the fact that they support the gills in water-breathing forms.

In all Craniata except the Cyclostomes the mandibular arch becomes modified into structures called *jaws* for the support of the mouth. Each mandibular bar divides into a dorsal and a ventral portion, called respectively the *palato-quadrate cartilage* (Fig. 719, A, *pal. qu.*) and *Meckel's cartilage* (*mck. c.*): the palato-quadrates grow forwards along the upper or anterior margin of the mouth, and unite with one another in the middle line, forming an *upper jaw:* Meckel's cartilages similarly extend along the lower or posterior margin of the mouth and unite in the middle line, forming the *lower jaw.* The *quadrate* (*qu*) or posterior end of the palato-quadrate furnishes an articulation for the lower jaw, and often acquires a connection with the cranium, thus serving to suspend the jaws from the latter. Thus each jaw arises from the union of paired bars, the final result being two unpaired transverse structures, one lying in the anterior, the other in the posterior margin of the transversely elongated mouth, and moving in a vertical plane. The fundamental difference between the jaws of a Vertebrate and the structures called by the same name in an Arthropod or a Polychætous Worm will be obvious at once.

The hyoid bar usually becomes divided into two parts, a dorsal, the *hyomandibular* or *pharyngo-hyal* (*hy.m.*), and a ventral, the *hyoid cornu*, which is again divisible from above downwards into segments called respectively *epi-hyal* (*ep.hy*), *cerato-hyal* (*c.hy*), and *hypo-hyal* (*h.hy*). The median ventral element of the arch, or *basi-hyal* (*b.hy*), serves for the support of the tongue. In some Fishes the hyomandibular articulates above with the auditory region of the cranium, while the jaws are connected with its ventral end. We may thus distinguish two kinds of *suspensorium* or jaw-suspending apparatus, a *mandibular suspensorium*, furnished by the quadrate, and a *hyoidean suspensorium* by the hyomandibular: in the former case the skull is said to be *autostylic*, *i.e.* having the jaw connected by means of its own arch, in the latter it is called *hyostylic:* in a few instances an *amphistylic* arrangement is produced by the articulation of both mandibular and hyoid arches with the skull.

The branchial arches become divided transversely into dorso-ventral segments called respectively *pharyngo-branchial* (*ph. br.*), *epi-branchial* (*ep.br.*), *cerato-branchial* (*c.br.*), and *hypo-branchial* *h.br.*), and the visceral skeleton thus acquires the character of an articulated framework which allows of the dilatation of the pharynx during swallowing and of its more or less complete closure at other times.

In connection with and always superficial to the rostrum, olfactory capsules, and jaws are frequently found *labial cartilages* (*lb. 1–4*), which sometimes attain a great size.

In the lower Fishes, such as Elasmobranchs, the cartilages of the skull become more or less encrusted by a superficial granular deposit of lime-salts, giving rise, as in the vertebral column, to *calcified cartilage*, but in all the higher forms true ossification takes place, the cartilaginous skull becoming complicated, and to a greater or less extent replaced, by distinct *bones*. Of these there are two kinds, *cartilage* and *membrane bones*. Cartilage bones begin by the deposition of minute patches of calcific matter in the cartilage itself: these *centres of ossification* are not distributed irregularly, but have definite positions, constant in the whole series of higher Craniata. As development proceeds, they may be replaced by ossification, starting in the *perichondrium*, or layer of connective tissue surrounding the cartilage, and gradually invading the latter. But in either case the bones in question are *preformed in cartilage, i.e.* replace originally cartilaginous parts. In the case of membrane bones centres of ossification appear, also in constant positions, in the fibrous tissue outside the cartilage: they may remain quite independent of the original cartilaginous skull and its cartilage bones, so as to be readily removable by boiling or maceration, or they may eventually become, as it were, grafted on to the cartilage, in which case all distinction between membrane and cartilage bones is lost in the adult. The membrane bones are to be looked upon as portions of the exoskeleton which have retreated from the surface and acquired intimate relations with the endoskeleton.

The cartilage bones have a very definite relation to the regions of the cartilaginous cranium. In the occipital region four bones are formed, surrounding the foramen magnum: a median ventral *basi-occipital* (Fig. 720, A and B, B. OC), paired lateral *ex-occipitals* (EX. OC), and a median dorsal *supra-occipital* (S. OC). In each auditory capsule three ossifications commonly appear: a *pro-otic* (A, PR. OT) in front, an *opisthotic* (OP. OT) behind, and an *epiotic* (EP. OT) over the arch of the posterior semicircular canal (*vide infra*). In front of the basi-occipital a bone called the *basi-sphenoid* (A and C, B. SPH) is formed in the floor of the skull: it appears in the position of the posterior ends of the trabeculæ, and bears on its upper or cranial surface a depression, the *sella turcica* (*s.t*), for the reception of the pituitary body. Connected on each side with the basi-sphenoid are paired bones, the *alisphenoids* (AL. SPH), which help to furnish the side walls of the interorbital region. The basi-sphenoid is continued forwards by another median bone, the *pre-sphenoid* (A and D, P. SPH), with which paired ossifications, the *orbito-sphenoids* (ORB. SPH), are connected, and complete the side walls of the interorbital region.

The basi-occipital, basi-sphenoid, and pre-sphenoid together form the basis cranii of the bony skull. A vertical plate of bone, the *mesethmoid* (M. ETH.), appears in the posterior portion of the cartilage of the same name, and the outer walls of the olfactory capsules may be ossified by paired *ecto-ethmoids* (E, EC. ETH).

So far, it will be seen, the cranial cavity has its hinder region alone roofed over by bone, *viz.* by the supra-occipital: for the rest of it the cartilage bones furnish floor and side walls only. This deficiency is made good by two pairs of membrane bones, the *parietals* (*PA*), formed immediately in front of the supra-occipital, and usually articulating below with the alisphenoids, and the

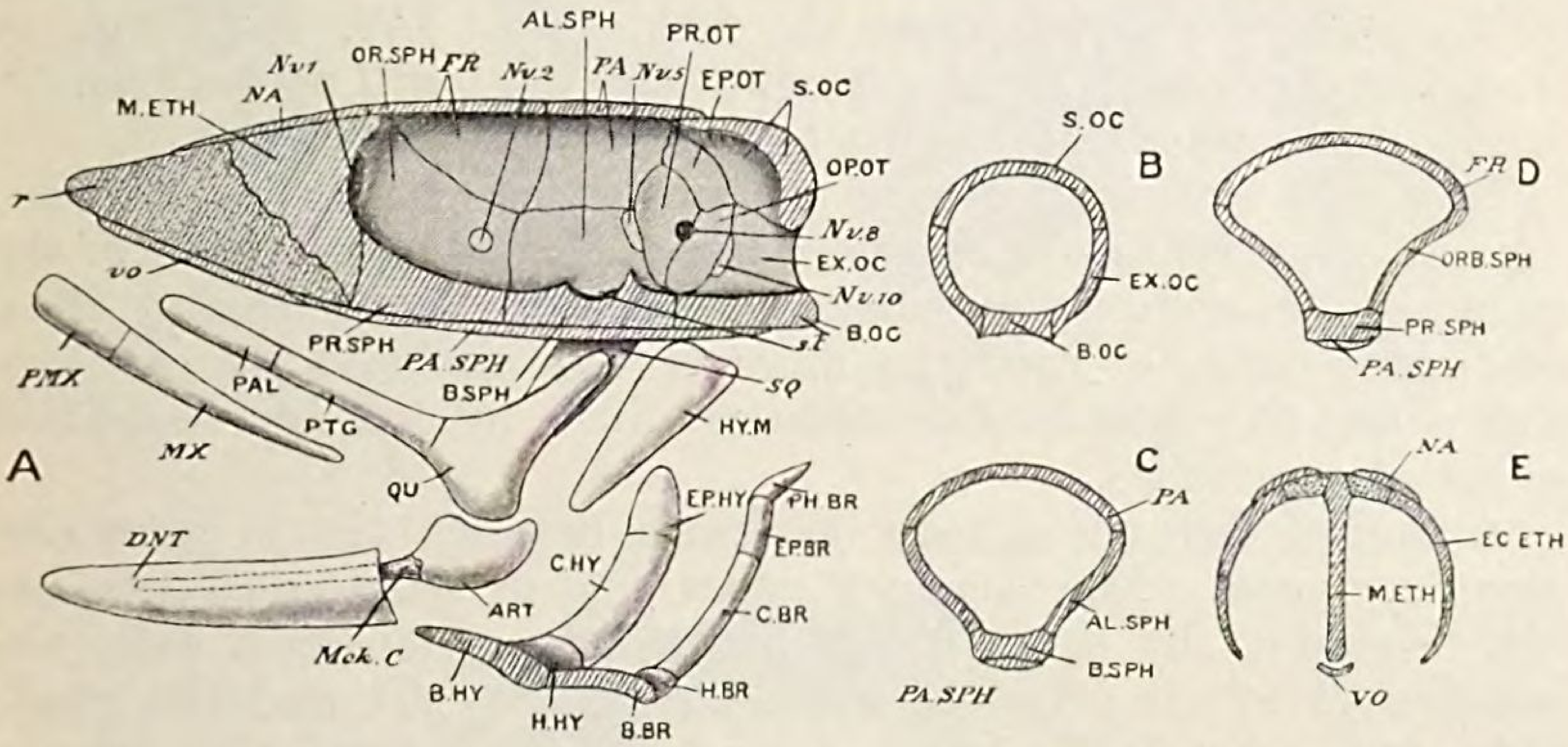


FIG. 720.—Diagram of bony skull in sagittal section; B, transverse section of occipital region; C, of parietal region; D, of frontal region; E, of ethmoidal region. Cartilaginous parts are dotted; cartilage bones are marked in thick type, membrane bones in italics; *mck. c.* Meckel's cartilage; *Nv. 1—10*, foramina for cerebral nerves; *r.* rostrum; *s. t.* sella turcica or pituitary fossa. Cartilage bones—**AL.SPH.** alisphenoid; **ART.** articular; **B. BR.** basi-branchial; **B. HY.** basi-hyal; **B. OC.** basi-occipital; **B. SPH.** basi-sphenoid; **C. BR.** cerato-branchial; **C. HY.** cerato-hyal; **EC.ETH.** ecto-ethmoid; **EP. BR.** epi-branchial; **EP. HY.** epi-hyal; **EX. OC.** ex-occipital; **H. BR.** hypo-branchial; **H. HY.** hypo-hyal; **HY.M.** hyomandibular; **M. ETH.** mesethmoid; **OP.OT.** opisthotic; **OR. SPH.** orbito-sphenoid; **PAL.** palatine; **PH. BR.** pharyngo-branchial; **PR.OT.** pro-otic; **PR. SPH.** pre-sphenoid; **PTG.** pterygoid; **QU.** quadrate; **S. OC.** supra-occipital. Membrane bones—*DNT.* dentary; *FR.* frontal; *MX.* maxilla; *NA.* nasal; *PA.* parietal; *PA.SPH.* parasphenoid; *PM.X.* premaxilla; *SQ.* squamosal; *VO.* vomer.

frontals (*FR*), placed in front of the parietals, and often connected below with the orbito-sphenoids. A pair of *nasals* (*NA*) are developed above the olfactory capsules and immediately in advance of the frontals; and below the base of the skull two important membrane bones make their appearance, the *vomer* (*VO*)—which may be double—in front, and the *parasphenoid* (*PA. SPH*) behind.

The result of the peculiar arrangement of cartilage and membrane bones just described is that the brain-case, in becoming ossified, acquires a kind of secondary segmentation, being clearly divisible in the higher groups, and especially in the Mammalia, into three quasi-segments. These are the *occipital segment* (*B*),

formed by the basi-occipital below, the ex-occipitals at the sides, and the supra-occipital above; the *parietal segment* (*C*), formed by the basi-sphenoid below, the alisphenoids laterally, and the parietals above; and the *frontal segment* (*D*) constituted by the pre-sphenoid below, the orbito-sphenoids on either side, and the frontals above. It must be observed that this segmentation of the cranium is quite independent of the primary segmentation of the head, which is determined by the presence of myomeres and by the relations of the cerebral nerves.

The cranial bones have constant relations to the cerebral nerves. The olfactory nerves (A, *Nv. 1*) pass out one on either side of the mesethmoid, the optic nerves (*Nv. 2*) through or immediately behind the orbito-sphenoids, the fifth nerves (*Nv. 5*) through or immediately behind the alisphenoids, and the tenth nerves (*Nv. 10*) through or immediately in front of the ex-occipitals.

It will be seen that a clear distinction can be drawn between the *primary cranium* or *chondrocranium*, formed by the fusion of the parachordals, auditory capsules, and trabeculæ, and consisting of an undivided mass of cartilage more or less replaced by cartilage bones, and the *secondary cranium* modified by the super-addition of membrane bones.

A similar distinction may be drawn between the *primary* and *secondary jaws*. The *primary upper jaw* or palato-quadrate becomes ossified by three chief cartilage bones on each side, the *palatine* (A, PL) in front, then the *pterygoid* (PTG), and the *quadrate* (QU) behind, the latter furnishing the articulation for the lower jaw or *mandible*. In the higher classes the primary upper jaw does not appear as a distinct cartilaginous structure, and the palatine and pterygoid are developed as membrane bones. The *secondary upper jaw* is constituted by two pairs of membrane bones, the *premaxilla* (*PMX*) and the *maxilla* (*MX*), which in bony skulls furnish the actual anterior boundary of the mouth, the primary jaw becoming altogether shut out of the gape. The proximal end o the *primary lower jaw* ossifies to form a cartilage bone, the *articular* (ART), by which the mandible is hinged; the rest of it remains as a slender, unossified *Meckel's cartilage* (*Mck. C*), which may disappear entirely in the adult. The *secondary lower jaw* is formed by a variable number of membrane bones, the most important of which is the *dentary* (*DNT*). In Mammalia the dentary forms the entire mandible, and articulates, not with the quadrate, but with a large membrane bone formed external to the latter, and known as the *squamosal* (*SQ*).

In the hyoid arch a cartilage bone, the *hyomandibular* (HY. M), appears in the cartilage of the same name, and ossifications are also formed in the various segments of the hyoid cornua (EP. HY, C. HY, H. HY, B. HY) and of the branchial arches (PH. BR, EP. BR, C. BR, H. BR, B. BR). In the air-breathing forms both hyoid and

branchial arches undergo more or less complete atrophy, the whole gill-bearing apparatus becoming reduced to a small *hyoid bone* serving for the support of the tongue.

The skeleton of the median fins is formed of a single row of cartilaginous rays or *pterygiophores* (Fig. 715, C and D, *f.r*), lying in the median plane and more numerous than the vertebræ. They may ossify, and may be supplemented by *dermal fin-rays*, formed either of bone or of a horn-like material, and developed in the

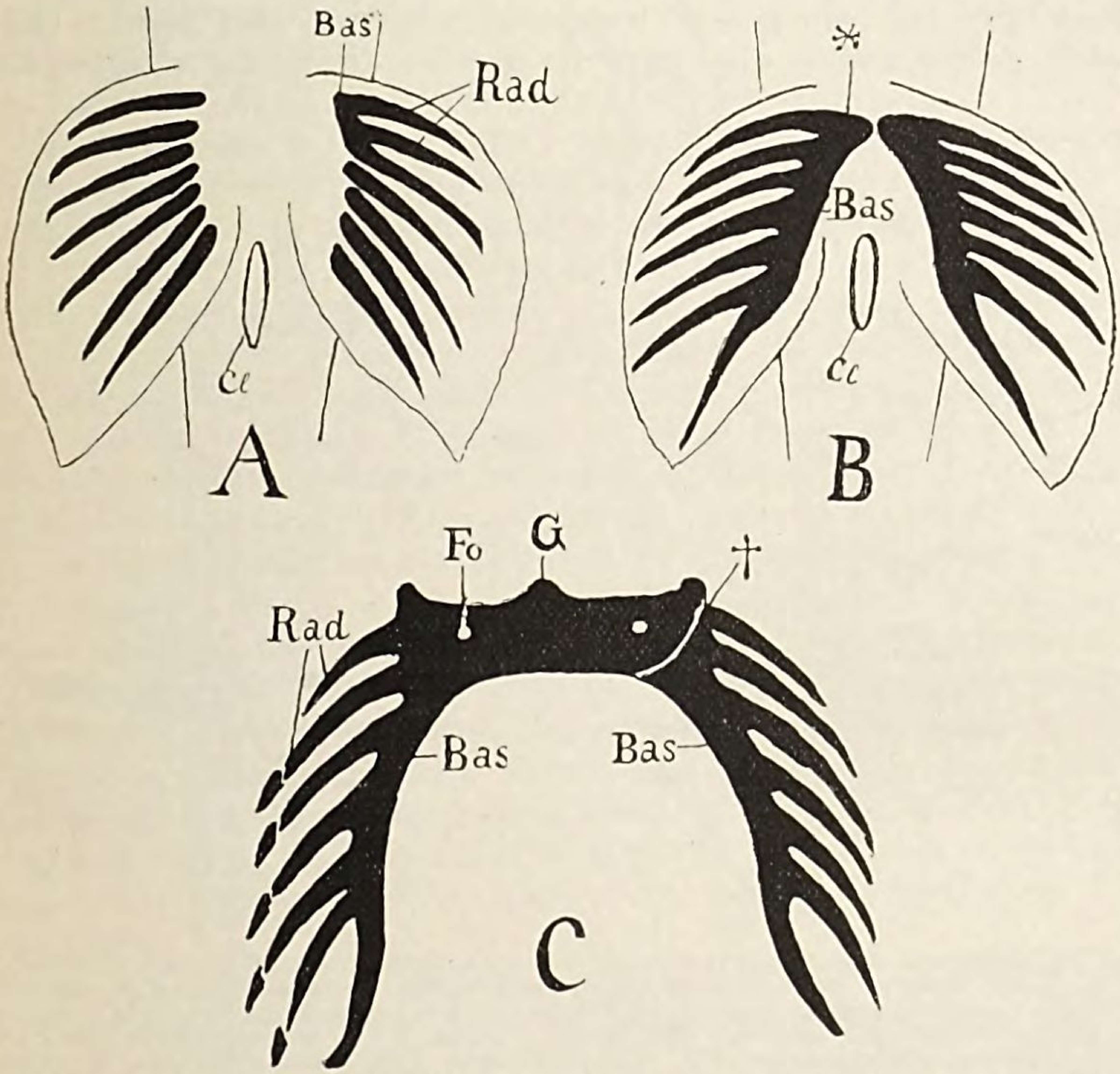


FIG. 721.—Diagram of three stages in the development of the pelvic fins. In A the anterior pterygiophores on the right side (*Rad*), have united to form a basal cartilage (*Bas.*); in B the basalia (*Bas.*) are fully formed and are uniting at * to form the pelvic girdle; in C the pelvic girdle (G) is fully constituted, and at † has segmented from the basale on the right side. *Cl.* cloacal aperture.

derm along the free edge of the fin. The latter are clearly exoskeletal structures.

As already mentioned, the paired fins are probably to be looked upon as the detached and enlarged anterior and posterior portions of a continuous lateral fin the intermediate portion of which has disappeared. Both pectoral and pelvic fins are supported by pterygiophores or *radialia* (Fig. 721, *Rad*), the basal or proximal ends of which are articulated with stout cartilages, often replaced

by cartilage bones, the *basalia* (*Bas*), which serve to strengthen the fin at its point of union with the trunk.

In all classes above Fishes the paired fins are, as we have seen, replaced by five-toed or *pentadactyle limbs*. These are supported by bones, probably to be looked upon as greatly modified pterygiophores, and obviously homologous in the fore- and hind-limbs. In the proximal division of each limb there is a single rod-like bone, the *humerus* (Fig. 722, A, HU), or upper arm bone in the fore-limb, the *femur* (B, FE), or thigh bone in the hind limb. In the middle division there are two elongated bones, an anterior, the *radius* (RA), and a posterior, the *ulna* (UL), in the fore-limb; an anterior, the

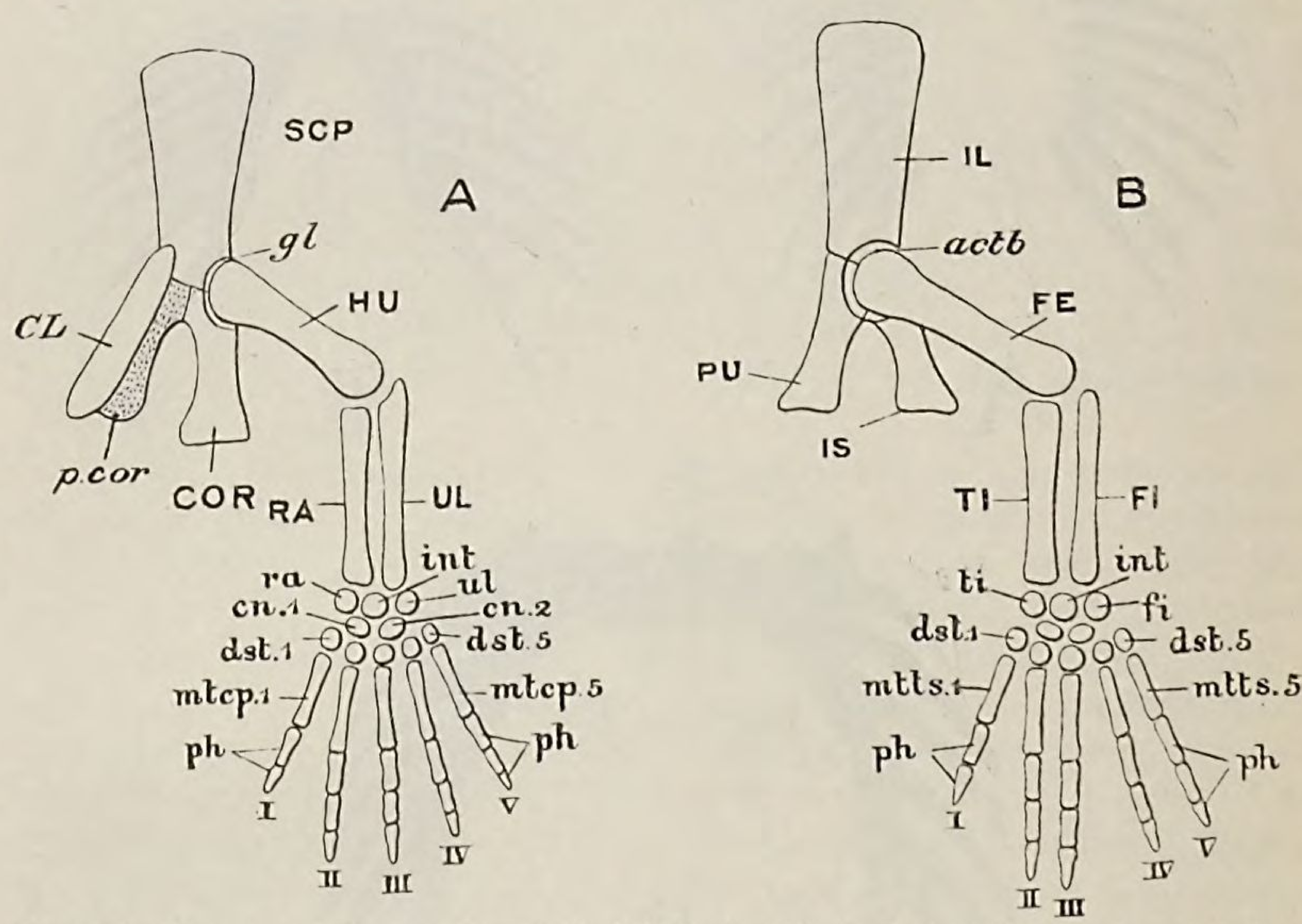


FIG. 722.—Diagrams of the fore (A) and hind (B) limbs with the limb-girdles. *actb.* acetabulum ; *gl.* glenoid cavity ; *p. cor.* procoracoid ; *I—V*, digits. Cartilage bones—**cn.1, cn.2,** centralia ; **COR.** coracoid ; **dst. 1—5,** distalia ; **FE.** femur ; **FI.** fibula ; **fi.** fibulare ; **HU.** humerus ; **IL.** ilium ; **int.** intermedium ; **IS.** ischium ; **mtcp. 1—5,** metacarpals ; **mt.ts.1—5,** metatarsals ; **ph.** phalanges ; **PU.** pubis ; **RA.** radius ; **ra.** radiale ; **TI.** tibia ; **ti.** tibiale ; **UL.** ulna ; **ul.** ulnare. Membrane bone—*CL.* clavicle.

tibia (TI), and a posterior, the *fibula* (FI), in the hind-limb. Next follow the bones of the hand and foot, which are again divisible into three sets: *carpals* or wrist-bones, *metacarpals* (mtcp) or hand-bones, and *phalanges* (ph) or finger-bones, in the fore-limb; *tarsals* or ankle-bones, *metatarsals* (B, mtts) or foot bones, and *phalanges* (ph) or toe-bones, in the hind-limb. The carpals and tarsals consist typically of three rows of small nodules of bone or cartilage. the proximal row containing three, the middle two, and the distal five elements. The three proximal carpals are called respectively *radiale* (A, ra), *intermedium* (int), and *ulnare* (ul), those of the middle row the first and second *centralia* (cn. 1,

cn. 2), those of the third row the five *distalia* (dst. 1–5), the separate elements being distinguished by numbers, counting from the anterior or radial edge of the limb. In the tarsus the bones of the first row are known respectively as *tibiale* (B, ti), *intermedium* (int), and *fibulare* (fi), those of the second row as *centralia* (cn. 1, cn. 2), and those of the third as *distalia* (dst. 1–5). The metacarpals (mtcp. 1–5) and metatarsals (mtts. 1–5) are five rod-like bones, one articulating with each distale: they are followed by the phalanges (ph), of which each digit may have from one to five. The first digit of the fore-limb (A, I) is distinguished as the *pollex* or thumb, that of the hind-limb (B, I) as the *hallux* or great toe; the fifth digit of each limb (V) is the *minimus*.

In connection with the paired appendages are formed supporting structures called the *limb-girdles;* they occur in the portions of the trunk adjacent to the appendages and serve for the articulation of the latter. In the embryonic condition they are continuous with the basalia and are probably to be looked upon as in-growths of the primitive fin-skeleton (Fig. 721). The *shoulder-girdle* or *pectoral arch* has primarily the form of paired bars, which may unite in the middle ventral line so as to form an inverted arch. Each bar—*i.e.* each half of the arch—furnishes a concave or convex *glenoid surface* (Fig. 722, A, *gl.*) for the articulation of the pectoral fin or fore-limb, and is thereby divided into two portions; a dorsal or *scapular region*, above the glenoid surface, and a ventral or *coracoid region* below it. The coracoid region is again divisible, in all classes above Fishes, into two portions: an anterior, the *procoracoid* (*p. cor*), and a posterior, the *coracoid* proper. Each of these regions commonly ossifies, a cartilage bone, the *scapula* (SCP), appearing in the scapular region, another, the *coracoid* (COR), in the coracoid region, while in relation with the procoracoid is formed a bone, the *clavicle* (*CL*), largely or entirely developed from membrane.

The constitution of the *hip-girdle*, or *pelvic arch*, is very similar. It consists originally of paired bars, which may unite in the middle ventral line, and are divided by the *acetabulum* (B, *actb.*), the articular surface for the pelvic fin or hind limb, into a dorsal or *iliac region*, and a ventral or *pubo-ischial region*, the latter being again divisible, in all classes above Fishes, into an anterior portion, or *pubis*, and a posterior portion, or *ischium*. Each region is replaced in the higher forms by a cartilage bone, the pelvic girdle thus consisting of a dorsal *ilium* (IL) serially homologous with the scapula, an antero-ventral *pubis* (PU) with the procoracoid and clavicle, and a postero-ventral *ischium* (IS) with the coracoid. The long bones of the limbs are divisible each into a *shaft*, and proximal and distal *extremities*. When ossification takes place the shaft is converted into a tubular bone the cartilaginous axis of which is absorbed and replaced by a vascular

fatty tissue called *marrow*. The extremities become simply calcified in the lower forms, but in the higher a distinct centre of ossification may appear in each, forming the *epiphysis*, which finally becomes ankylosed to the shaft.

Digestive Organs.—The *enteric canal* is divisible into buccal cavity (Fig. 715, A, *buc. c.*), pharynx (*ph.*), gullet, stomach (*st.*), and intestine (*int.*), the latter sometimes communicating with the exterior by a cloaca (*cl.*), which receives the urinary and genital ducts. The *buccal cavity* is developed from the stomodæum of the embryo: the proctodæum gives rise to a very small area in the neighbourhood of the anus, or, when a cloaca is present, to its external portion: all the rest of the canal is formed from the mesenteron, and is therefore lined by an epithelium of endodermal origin. The *pharynx* communicates with the exterior, in Fishes and in the embryos of the higher forms, by the gill-slits (*i. br. a.* 1–7); it communicates with the stomach by a comparatively narrow *gullet*. The *stomach* (*st.*) is usually bent upon itself in the form of a U; the *intestine* (*int.*) is generally more or less convoluted; hence the stomach and intestine are together considerably longer than the enclosing abdominal cavity. In the embryo the intestine is sometimes continued backwards into the hæmal canal by an extension called the *post-anal gut* (*p. a. g.*), which may be taken to indicate that the anus has shifted forwards in the course of evolution.

The epithelium of the buccal cavity is usually many-layered, like that of the skin, of which it is developmentally an in-turned portion; the pharynx and gullet have also a laminated epithelium, but the rest of the canal is lined by a single layer of cells (Fig. 723, E) underlaid by a loose layer of connective tissue, the *sub-mucosa* (*Z*); epithelium and sub-mucosa together constitute the *mucous membrane*. The mucous membrane of the stomach and sometimes of the intestine contains close-set tubular glands (*D*); those of the stomach, the *gastric glands*, secrete *gastric juice*, which acts upon the proteid portions of the food only; the *intestinal glands* digest proteids, starch, and fats. Outside the mucous membrane are layers of *unstriped muscle*, usually an internal circular (*M'*) and an external longitudinal (*M*) layer. Externally the intra-cœlomic portion of the canal is invested by peritoneum (*B*) formed of a layer of connective tissue next the gut and a single-layered cœlomic epithelium facing the body-cavity.

In connection with the enteric canal certain very characteristic structures are developed. In the mucous membrane of the mouth calcifications appear and form the *teeth*, which usually occur in a row along the ridge of each jaw, but may be developed on the roof of the mouth, on the tongue, and even in the pharynx. A tooth is usually formed of three tissues—*dentine*, *enamel*, and

cement. The main bulk of the tooth is made of dentine (Fig. 724, B, *ZB*), which occurs under three forms. *Hard dentine* consists of a matrix of animal matter strongly impregnated with lime salts and permeated by delicate, more or less parallel, tubules containing organic fibrils. *Vaso-dentine* is permeated with blood-vessels, and consequently appears red and moist in the fresh condition. *Osteo-dentine* approaches in its structure and mode of

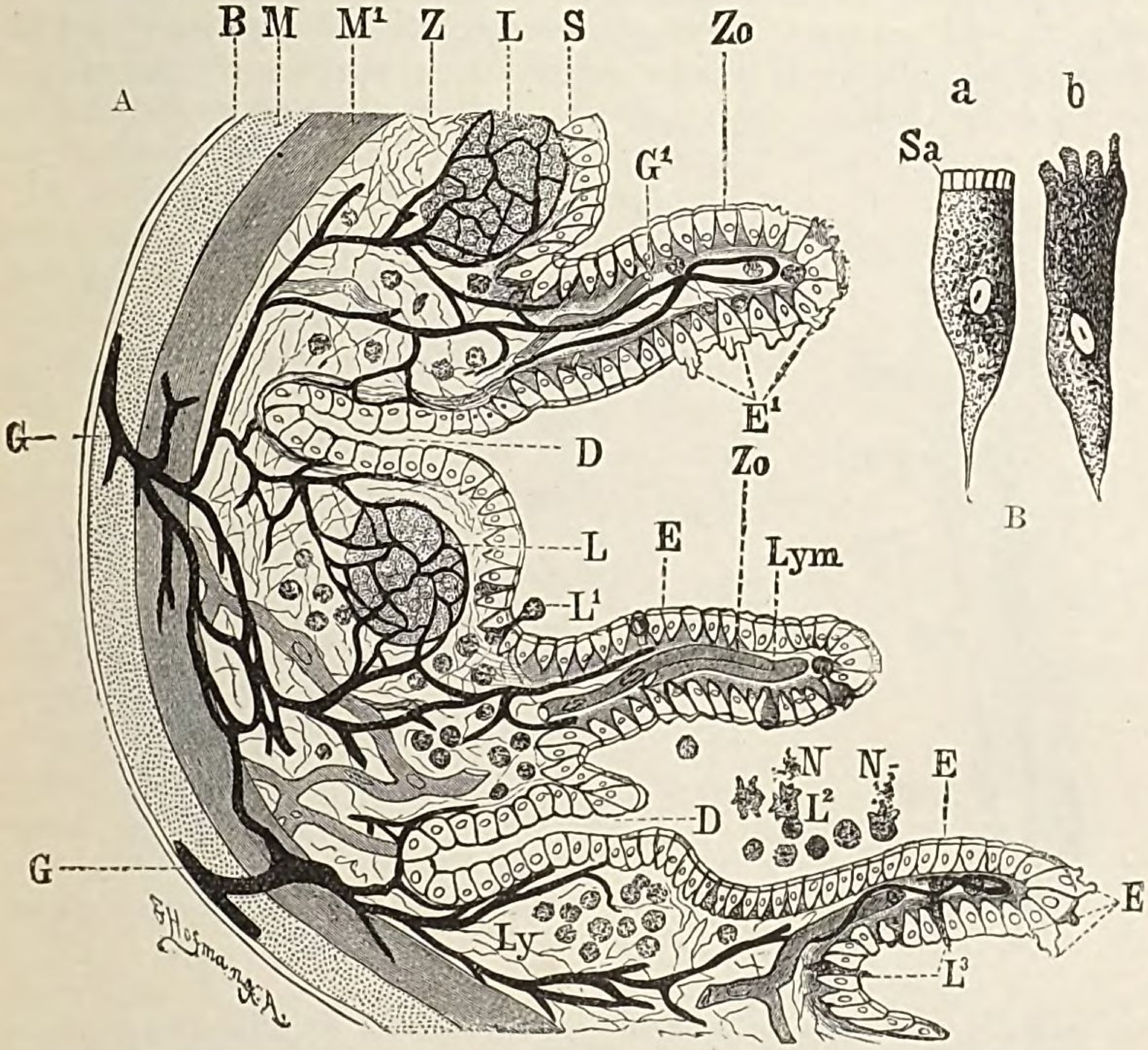


FIG. 723.—A, semi-diagrammatic transverse section of the intestine of a **Craniate**; B, two epithelial cells, highly magnified. *B*, visceral layer of peritoneum; D, tubular glands; *E*, columnar epithelium (magnified at B, a); E^1, the same with amœboid processes (magnified at B, b); G, G^1, blood-vessels; L, lymph-follicles; L^1—L^3, Ly, lymph-cells; *Lym*, lacteals; M, longitudinal muscular layer; M′, circular muscular layer; N, nutritive matters in cavity of intestine being ingested by wandering lymph-cells; *Sa*, striated border of epithelial cells; *z*, sub-mucosa; *Zv* villus. (From Wiedersheim's *Vertebrata.*)

development to bone. The free surface of the tooth is usually capped by a layer of enamel (*ZS*), a dense substance, either structureless or presenting a delicate fibrillation, containing not more than 3 to 5 per cent. of animal matter, and being therefore the hardest tissue in the body. The cement (*ZC*) coats that portion of the tooth which is embedded in the tissues of the jaw, and sometimes forms a thin layer over the enamel; it has practically the structure of bone. At the inner end of the tooth there

is frequently an aperture (*PH'*) leading into a cavity (*PH*) filled, in the fresh condition, by the *tooth-pulp*, a sort of connective tissue plug abundantly supplied with nerves and blood-vessels.

In the development of a tooth (Fig. 724, B) the deep layer of the buccal epithelium becomes invaginated and grows inwards or into the sub-mucosa in the form of a narrow cord, the *enamel organ* (*SK*). The distal end of this enlarges into a flask-like form, and the bottom of the flask becomes invaginated (*MA*) by the growth of a conical process of the sub-mucosa, the *dental papilla* (*ZK*). Mesoderm cells accumulate on the free surface of the papilla and form a distinct layer of cells called *odontoblasts* (*O*). From

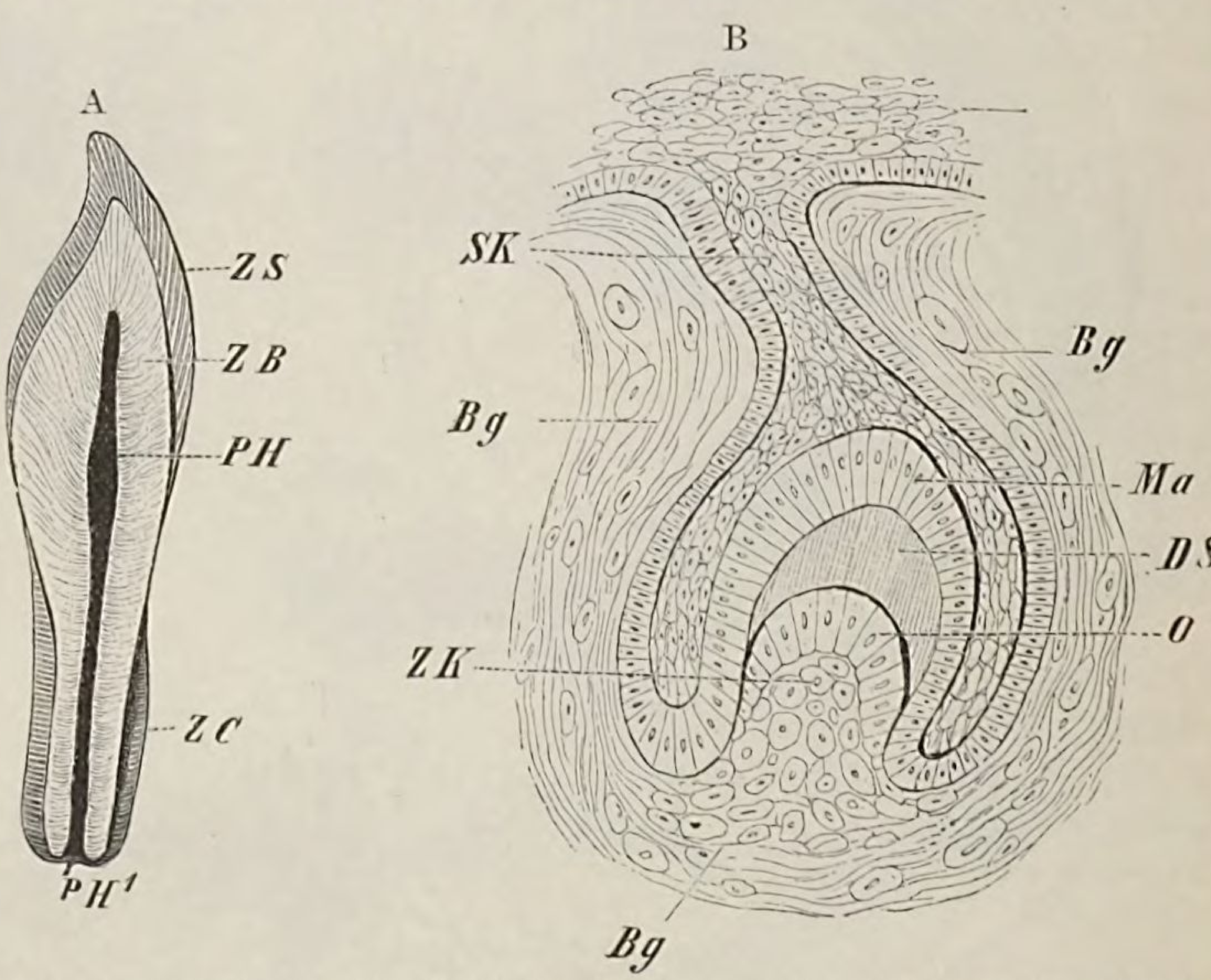


FIG. 724.—A, longitudinal section of a tooth, semi-diagrammatic. *PH*, pulpcavity; *PH'*, opening of same; *ZB*, dentine; *ZC*, cement; *ZS*, enamel. B, longitudinal section of developing tooth; *Bg*, submucosa; *DS*, dentine; *MA*, invaginated layer of enamel organ; *ME*, epithelium of mouth; *O*, odontoblasts; *SK*, stalk of enamel organ; *ZK*, tooth-papilla. (From Wiedersheim's *Vertebrata*.)

these the dentine is formed in successive layers which gradually accumulate between the layer of odontoblasts and the inner or invaginated layer of the enamel organ. The lower, or proximal, part of the papilla remains uncalcified and forms the tooth-pulp. The enamel is formed by the deposition of successive layers of calcific matter from the inner or invaginated layer of the enamel organ, the cement by the ossification of the tissue immediately surrounding the papilla. Thus the tooth is partly of ectodermal, partly of mesodermal, origin.

In some Fishes the scales or elements of the dermal exoskeleton, pass insensibly into the teeth over the ridges of the

jaws and agree with them in structure, so that there can be no doubt as to the homology of the two. Teeth are, in fact, to be looked upon as portions of the exoskeleton which have migrated from the skin into the buccal cavity, and even into the pharynx, and have there increased in size and assumed special functions.

The *tongue* is a muscular elevation of the floor of the mouth, supported by the basi-hyal, and usually more or less protrusible. The roof of the buccal cavity in the embryo sends off a pouch, the *pituitary diverticulum* (Fig. 715, A, *pty. s.*), which grows upwards and, losing its connection with the mouth, becomes attached to the ventral surface of the brain as the *pituitary body* (*pty. b.*). It may correspond with the sub-neural gland of Urochorda.

In terrestrial Craniata *buccal glands* are present, opening by ducts into the mouth: the most important of these are the racemose *salivary glands* which secrete a digestive fluid, *saliva*, capable of converting starch into sugar. There are also two large and highly characteristic digestive glands in the abdominal cavity, both developed as outpushings of the intestine, but differing greatly from one another, in their fully developed state, both in outward appearance and in histological structure: these are the *liver* and the *pancreas*.

The liver is (Fig. 715, A, *lr.*) a dark-red organ of relatively immense size: it not only secretes a digestive juice, the *bile*, which has the function of emulsifying fats, but also forms an amyloid substance called *glycogen* or animal starch, which, after being stored up in the liver-cells, is restored to the blood in the form of sugar. The liver is formed of a mass of polyhedral cells (Fig. 725, *l.*) with minute intercellular spaces which receive the bile secreted from the cells and from which it passes to the ducts (*b*). The pancreas (Fig. 715, A, *pn.*) is a racemose gland, and secretes *pancreatic juice*, which acts upon proteids, starch, and fats. The ducts of both glands usually open into the anterior end of the intestine: that of the liver (*b. d.*) generally gives off a blind offshoot ending in a capacious dilatation,

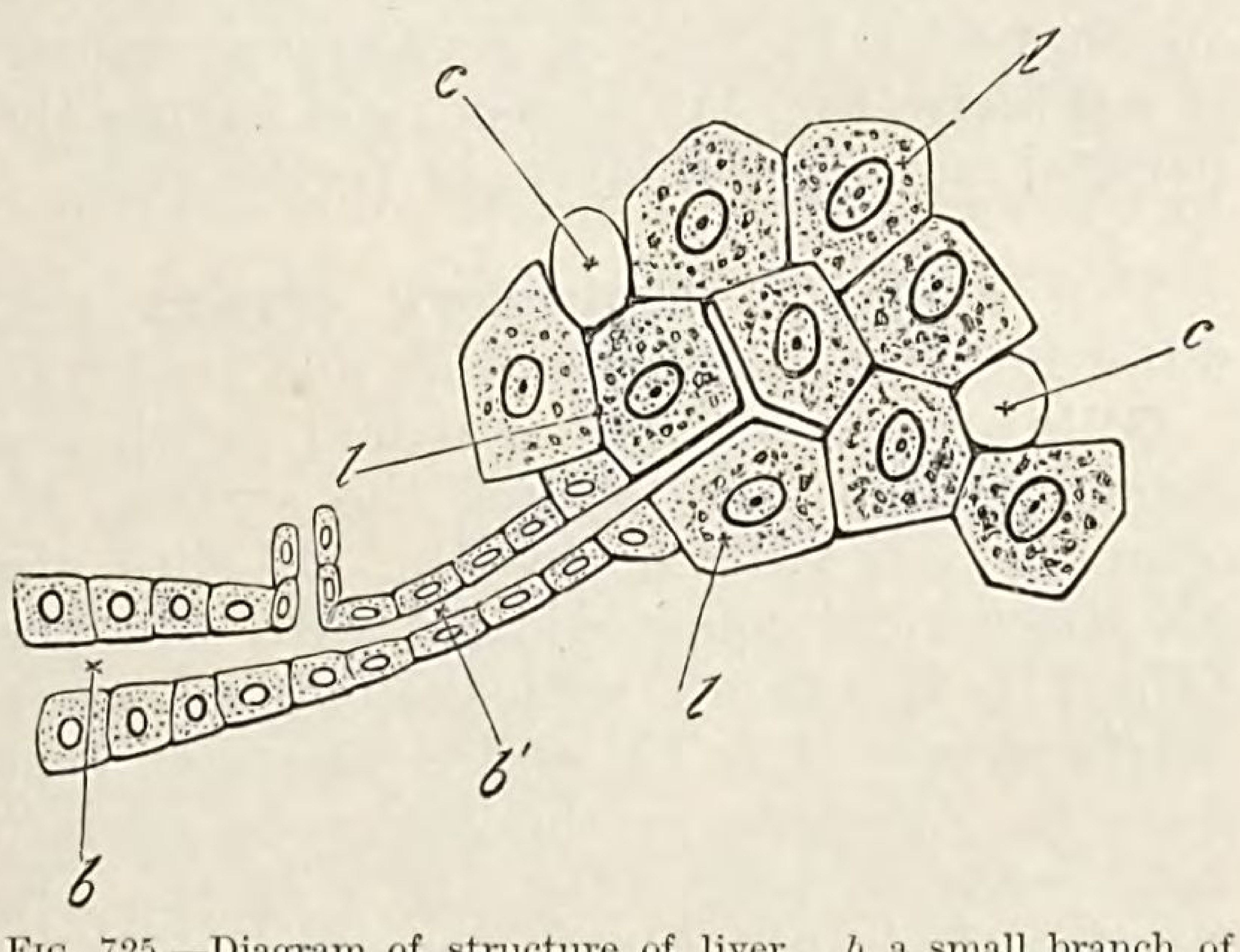


FIG. 725.—Diagram of structure of liver. *b*, a small branch of hepatic duct; *b'*, its ultimate termination in the intercellular spaces; *c*, blood capillaries; *l*, liver cells. (From Huxley's *Physiology*.)

the *gall-bladder* (*g. b.*), in which the bile is stored. We thus have one or more *hepatic ducts* conveying the bile from the liver and meeting with a *cystic duct* from the gall-bladder, while from the junction a *common bile duct* leads into the intestine.

Another important and characteristic organ in the abdomen of Craniata is the *spleen* (*spl.*), a gland-like organ of variable size and shape, attached to the stomach by a fold of peritoneum, but having no duct. It is formed of a pulpy substance containing numerous red blood-corpuscles, many of them in process of disintegration: dispersed through the pulp are masses of leucocytes which multiply and pass into the veins.

Two other *ductless glands* are formed in connection with the enteric canal. The *thyroid* (*thd.*) is developed as an outpushing of the floor of the pharynx which becomes shut off and forms, in the adult, a gland-like organ of considerable size. Its final position varies considerably in the different classes. It has been compared with the endostyle of Tunicata, which, as will be remembered, is an open groove on the ventral side of the pharynx.

The *thymus* is developed from the epithelium of the dorsal ends of the gill-clefts: in the adult it may take the form of a number of separate gland-like bodies lying above the gills, or may be situated in the neck or even in the thorax. The functions of both thyroid and thymus are very imperfectly understood.

The whole intra-abdominal portion of the enteric canal as well as the liver, pancreas, spleen, and indeed all the abdominal viscera, are supported by folds of peritoneum, called by the general name of *mesentery* (Fig. 715, C, *mes.*) and having the usual relation to the parietal and visceral layers of peritoneum.

Two kinds of **respiratory organs** are found in Craniata: water-breathing organs or *gills*, and air-breathing organs or *lungs*.

Gills arise as a series of paired pouches of the pharynx which extend outwards or towards the surface of the body and finally open on the exterior by the gill-slits already noticed. Each *gill-pouch* thus communicates with the pharynx by an *internal* (Fig. 715, B, *i. br. a.*), with the outside water by an *external branchial aperture* (*e. br. a*), and is separated from its predecessor and from its successor in the series by stout fibrous partitions, the *inter-branchial septa* (Fig. 726, *i. br. s*). The mucous membrane forming the anterior and posterior walls of the pouches is raised up into a number of horizontal ridges, the *branchial filaments* (*br. f.*), which are abundantly supplied with blood. A current of water entering at the mouth passes into the pharynx, thence by the internal gill-slits into the gill-pouches, and finally makes its way out by the external gill-slits, bathing the branchial filaments as it goes. The exchange of carbonic acid for oxygen takes place in the blood-vessels of the branchial filaments, which are, therefore,

the actual organs of respiration. It will be noticed that the respiratory epithelium is endodermal, being derived from that of the pharynx, which, as we have seen, is a portion of the mesenteron.

As already mentioned, the walls of the pharynx are supported by the visceral arches, which surround it like a series of incomplete hoops, each half-arch or visceral bar being embedded in the inner or pharyngeal side of an inter-branchial septum. Thus the visceral arches (*v. b.*) alternate with the gill-pouches, each being related to the posterior set of filaments of one pouch and the anterior set of the next. In the higher Fishes, such as a Trout or Cod, the inter-branchial septa become reduced to narrow bars enclosing the visceral arches (right side of Fig. 726), with the result that a double set of free branchial filaments springs from each visceral bar and constitutes what is called a single *gill*. Thus an entire gill or *holobranch* (*hl. br.*) is the morphological equivalent of two half-gills, *hemibranchs*, or sets of branchial filaments, belonging to the adjacent sides of two consecutive gill-pouches. On the other hand, a gill-pouch is equivalent to the posterior hemibranch of one gill and the anterior hemibranch of its immediate successor.

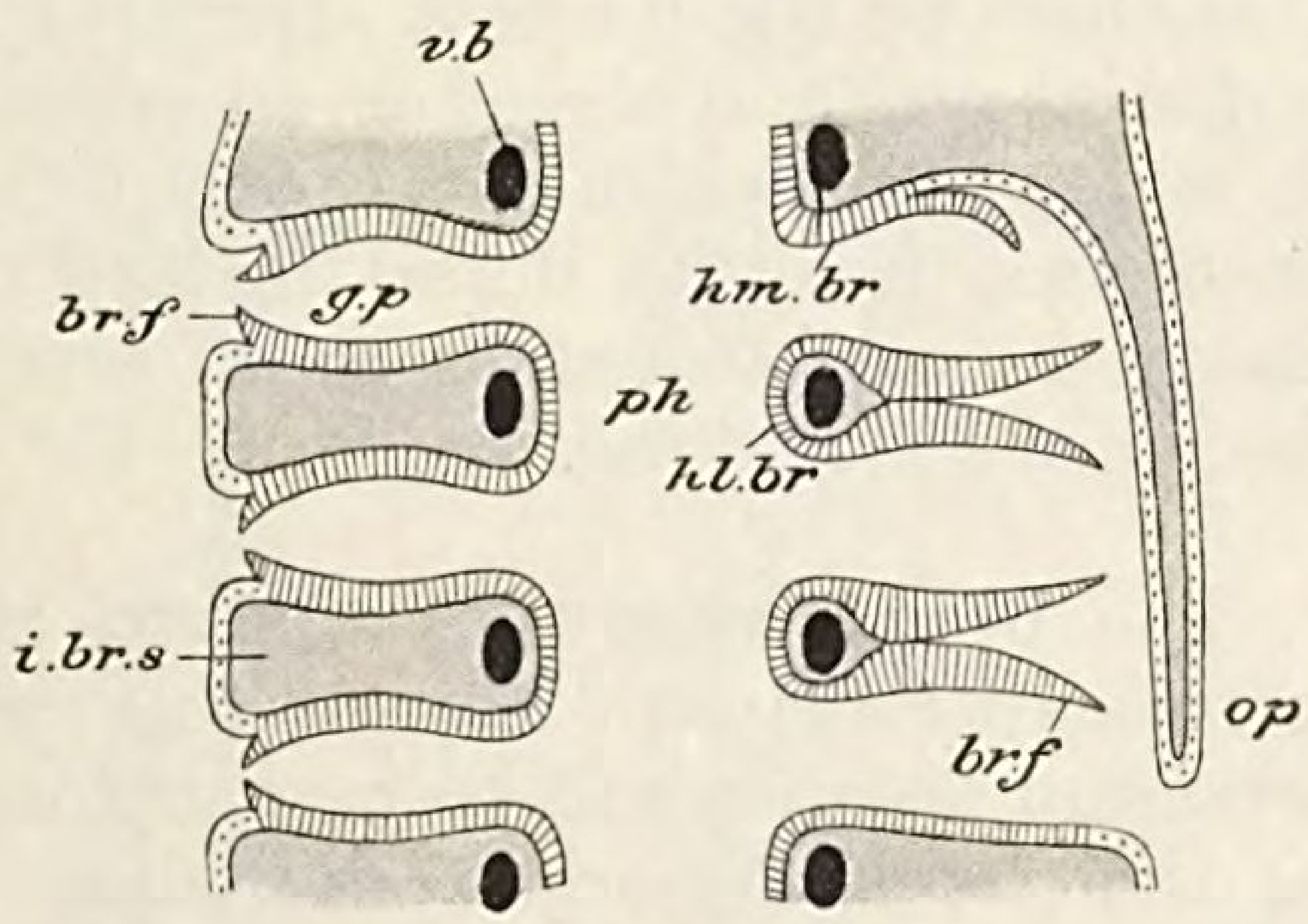


FIG. 726.—Diagrammatic horizontal section of the pharyngeal region of a **Craniate**: on the left are shown three gill-pouches (*g. p.*) with fixed branchial filaments (*br. f.*) and separated by inter-branchial septa (*i. br. s.*); on the right one hemibranch (*hm. br.*) and two holobranchs (*hl. br.*) with free filaments, covered by an operculum (*op.*). Ectoderm dotted, endoderm striated, mesoderm evenly shaded, visceral bars (*v. b.*) black.

In some Amphibia water-breathing organs of a different type are found. These are the *external gills* (Fig. 886, *bis*): they are developed as branched outgrowths of the body-wall in immediate relation with the gill-slits, and differ from the internal gills just described in having an ectodermal epithelium. They are, therefore, comparable with the gills of Chætopods or Crustacea.

Lungs (Fig. 715, A, *lg*) are found in all Craniata, from the Dipnoi upwards. They are developed as a hollow outpushing from the ventral wall of the pharynx, which passes backwards and upwards, usually dividing into right and left divisions, and finally coming to lie in the dorsal region of the cœlome. The inner surface of the single or double lung thus formed is raised into a more or less complex network of ridges so as to increase the surface of blood exposed to the action of the air; and, in the higher forms, the ridges, increasing in number and complexity, and uniting with one another across the lumen of the lung, convert it into a sponge-like

structure. The respiratory epithelium is, of course, endodermal. Since the lungs are blind sacs, some contrivance is necessary for renewing the air contained in them: this is done either by a process analogous to swallowing, or by the contraction and relaxation of the muscles of the trunk.

In some Fishes there occurs, in the position occupied in air-breathers by the lungs, a structure called the **air-bladder**, which contains gas, and serves as an organ of flotation. Like the lungs, it is developed as an outgrowth of the pharynx, but, except in two instances, from its dorsal instead of its ventral side. In many cases the air-bladder loses its connection with the pharynx and becomes a closed sac.

The **blood vascular system** attains a far higher degree of complexity than in any of the groups previously studied: its essential features will be best understood by a general description of the circulatory organs of Fishes.

The *heart* (Figs. 715 and 727) is a muscular organ contained in the pericardial cavity and composed of three chambers, the *sinus venosus* (*s. v.*), the *auricle* (*au.*), and the *ventricle* (*v.*), which form a single longitudinal series, the hindmost, the sinus venosus, opening into the auricle, and the auricle into the ventricle. They do not, however, lie in a straight line, but in a zigzag fashion, so that the sinus and auricle are dorsal in position, the ventricle ventral. Sometimes a fourth chamber, the *conus arteriosus* (*c. art.*), is added in front of the ventricle. The various chambers are separated from one another by valvular apertures (Fig. 728) which allow of the flow of blood in one direction only, *viz.* from behind forwards, or from sinus to auricle, auricle to ventricle, and ventricle to conus. The heart is made of striped muscle—the only involuntary muscle in the body having this histological character—which is particularly thick and strong in the ventricle. It is lined internally by epithelium and covered externally by the visceral layer of the pericardium.

Springing from the ventricle, or from the conus when that chamber is present, and passing directly forwards in the middle line below the gills, is a large, thick-walled, elastic blood-vessel, the *ventral aorta* (Figs. 715, B, and 727, *v. ao.*), formed of fibrous and elastic tissue and unstriped muscle, and lined with epithelium. At its origin, which may be dilated, forming a *bulbus aortæ*, are valves so disposed as to allow of the flow of blood in one direction only, *viz.* from the ventricle into the aorta. It gives off on each side a series of half-hoop-like vessels, the *afferent branchial arteries* (*a. br. a.*), one to each gill. These vessels ramify extensively, and their ultimate branches open into a network of microscopic tubes or *capillaries* (Fig. 728, G.), having walls formed of a single layer of epithelial cells, which permeate the connective-tissue layer of the branchial filaments, and have therefore nothing between

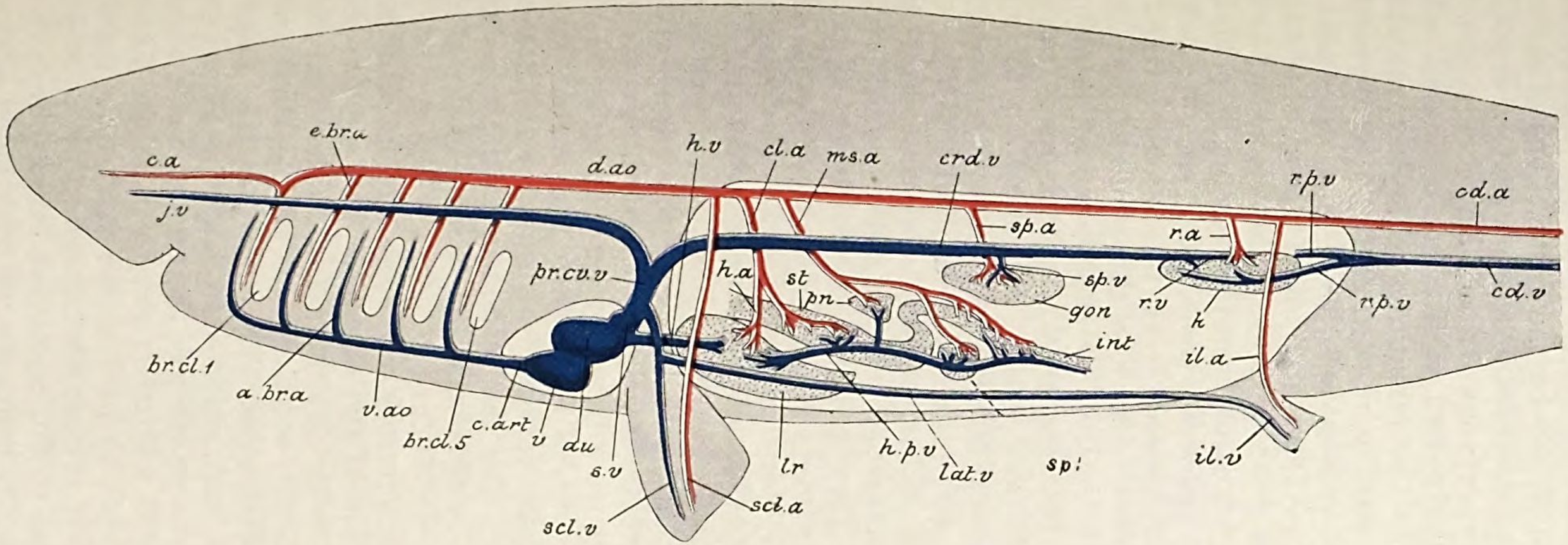


FIG. 727.—Diagram of the vascular system of a **Fish.** Vessels containing aërated blood red, those containing non-aërated blood blue. *a. br. a.* afferent branchial artery; *au.* auricle; *br. cl. 1—5*, branchial clefts; *c. a.* carotid artery; *c. art.* conus arteriosus; *cd. a.* caudal artery; *cd. v.* caudal vein; *cl. a.* cœliac artery; *crd. v.* cardinal vein; *d. ao.* dorsal aorta; *e. br. a.* efferent branchial artery; *gon.* gonad; *h. a.* hepatic artery; *h. p. v.* hepatic portal vein; *h. v.* hepatic vein; *il. a.* iliac artery; *il. v.* iliac vein; *int.* intestine; *j. v.* jugular vein; *k.* kidney; *lr.* liver; *lat. v.* lateral vein; *ms. a.* mesenteric artery; *pn.* pancreas; *pr. cv. v.* pre-caval vein; *r. a.* renal artery; *r. p. v.* renal portal vein; *r. v.* renal vein; *scl. a.* subclavian artery; *scl. v.* subclavian vein; *sp. a.* spermatic artery; *spl.* spleen; *sp. v.* spermatic vein; *st.* stomach; *s. v.* sinus venosus; *v.* ventricle; *v. ao.* ventral aorta.

them and the surrounding water but the epithelium of the filaments. The blood, driven by the contractions of the heart into the ventral aorta, is pumped into these respiratory capillaries, and there exchanges its superfluous carbonic acid for oxygen. It then passes from the capillaries into another set of vessels which join with one another, like the tributaries of a river, into larger and larger trunks, finally uniting, in each gill, into an *efferent branchial artery* (*e. br. a.*). The efferent arteries of both sides pass upwards and discharge into a median longitudinal vessel, the *dorsal aorta* (*d. ao.*), situated immediately beneath the notochord or vertebral column. From this trunk, or from the efferent branchial arteries, numerous vessels, the *systemic arteries*, are given off to all parts of the body, the most important being the *carotid arteries* (*c. a.*) to the head, the *subclavian* (*scl. a.*) to the pectoral fins, the *cœliac* (*cl. a.*) and *mesenteric* (*ms. a.*) to the stomach, intestine, liver, spleen, and pancreas, the *renal* (*r. a.*) to the kidneys, the *spermatic* (*sp. a.*) or *ovarian* to the gonads, and the *iliac* (*il. a.*) to the pelvic fins. After giving off the last the aorta is continued as the *caudal artery* (*cd. a.*) to the end of the tail.

With the exception of the capillaries, all the vessels described in the preceding paragraph, including the dorsal and ventral aortæ, are *arteries*. They are firm, elastic tubes, do not collapse when empty, usually contain but little blood in the dead animal, and serve to carry the blood from the heart to the body generally.

The systemic arteries branch and branch again into smaller and smaller trunks and finally pour their blood into a capillary network (Fig. 728, B, K, and T) with which all the tissues of the body, except epithelium and cartilage, are permeated. In these *systemic capillaries* the blood parts with its oxygen and nutrient constituents to the tissues and receives from them the various products of destructive metabolism, carbonic acid, water, and nitrogenous waste. The systemic, like the respiratory, capillaries are microscopic, and their walls are formed of a single layer of epithelial cells.

We saw that the respiratory capillaries are in connection with two sets of vessels, afferent and efferent. The same applies to the systemic capillaries, with the important difference that their efferent vessels are not arteries, but thin-walled, non-elastic collapsible tubes called *veins*. They receive the impure blood from the capillaries and unite into larger and larger trunks, finally opening into one or other of the great veins, presently to be described, by which the blood is returned to the heart. As a general rule the vein of any part of the body runs parallel to its artery, from which it is at once distinguished by its wider calibre, by its dark colour, due to the contained bluish-purple blood seen through its thin walls, by being gorged with blood after death, by the complete collapse of its walls when empty, and by its usually

containing valves. In some cases the veins become dilated into spacious cavities called *sinuses;* but sinuses without proper walls, such as occur in many Invertebrates, are never found in the Craniata.

The veins from the head join to form large, paired *jugular veins* (*j. v.*) which pass backwards, one on each side of the head, and are joined by the *cardinal veins* (*crd. v.*) coming from the trunk, each jugular uniting with the corresponding cardinal to form a large *precaval vein* (*pr. cv. v.*) which passes directly downwards and enters the sinus venosus. The blood from the tail returns by a *caudal vein* (*cd. v.*), lying immediately below the caudal artery in the hæmal canal of the caudal vertebræ (Fig. 715, D). On reaching the cœlome the caudal vein forks horizontally, and the two branches either become directly continuous with the cardinals or pass one to each kidney under the name of the *renal portal veins* (Fig. 727, *r. p. v.*). In the kidneys they break up into capillaries (Fig. 728, K), their blood mingling with that brought by the renal arteries and being finally discharged into the cardinals by the *renal veins* (*r. v*). Thus the blood from the tail may either return directly to the heart in the normal manner or may go by way of the capillaries of the kidneys. In the latter case there is said to be a *renal portal system*, the essential characteristic of which is that the kidney has a double blood supply, one of pure blood from the renal artery, and one of impure blood from the renal portal vein; in other words, it has two afferent vessels, an artery and a vein, and the latter is further distinguished by the fact that it both begins and ends in capillaries instead of beginning in capillaries and ending in a vein of higher order.

The blood from the gonads is returned to the cardinals by veins called *spermatic* (*sp. v.*) in the male, *ovarian* in the female. That from the paired fins takes, in what appears to be the most typical case, a somewhat curious course. On each side of the body there is a *lateral vein* (*lat. v.*), running in the body wall and following the course of the embryonic ridge between the pectoral and pelvic fins. It receives, anteriorly, a *subclavian vein* (*scl. v.*) from the pectoral fin, and posteriorly an *iliac vein* (*il. v.*) from the pelvic fin, and in front pours its blood into the precaval.

The veins from the stomach, intestine, spleen, and pancreas join to form a large *hepatic portal vein* (*h. p. v.*), which passes to the liver and there breaks up into capillaries, its blood mingling with that brought to the liver by the *hepatic artery* (*h. a.*), a branch of the cœliac. Thus the liver has a double blood supply, receiving oxygenated blood by the hepatic artery, and non-oxygenated, but food-laden, blood by the hepatic portal vein (Fig. 728, L). In this way we have a *hepatic portal system* resembling the renal portal system both in the double blood supply, and in the fact

that the afferent vein terminates, as it originates, in capillaries. After circulating through the liver the blood is poured, by *hepatic veins* (*h. v.*), into the sinus venosus. The hepatic, unlike the renal, portal system, is of universal occurrence in the Craniata.

In the embryo there is a *sub-intestinal vein*, corresponding with that of Amphioxus, and lying beneath the intestine and the post-anal gut. Its posterior portion becomes the caudal vein of the adult, its anterior portion one of the factors of the hepatic portal vein.

To sum up: the circulatory organs of the branchiate Craniata consist of (*a*) a muscular organ of propulsion, the *heart*, provided with valves and driving the blood into (*b*) a set of thick-walled, elastic, afferent vessels, the *arteries*, from which it passes into (*c*) a network of microscopic vessels or *capillaries* which permeate the

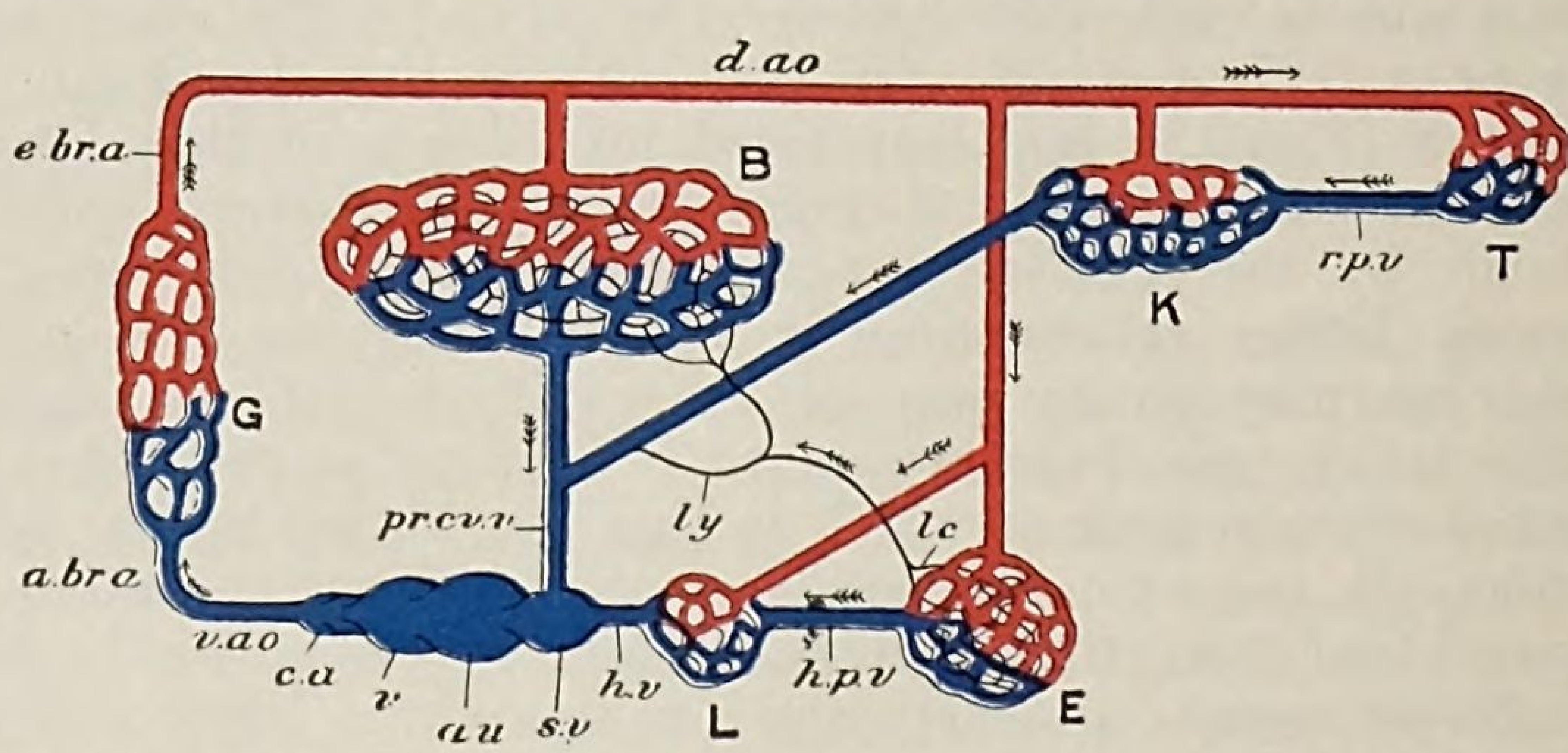


FIG. 728.—Diagram illustrating the course of the circulation in a **Fish.** Vessels containing aërated blood red, those containing non-aërated blood blue, lymphatics black. B. capillaries of the body generally; E. of the enteric canal; G. of the gills; K. of the kidneys; L. of the liver; T. of the tail. *a. br. a.* afferent branchial arteries; *au.* auricle; *c. a.* conus arteriosus; *d. ao.* dorsal aorta; *e. br. a.* efferent branchial arteries; *h. p. v.* hepatic portal vein; *h. v.* hepatic vein; *lc.* lacteals; *ly.* lymphatics; *pr. cv. v.* pre-caval veins; *r. p. v.* renal portal veins; *s. v.* sinus venosus; *v.* ventricle; *v. ao.* ventral aorta. The arrows show the direction of the current.

tissues, supplying them with oxygen and nutrient matters and receiving from them carbonic acid and other waste products: from the capillary network the blood is carried off by (*d*) the *veins*, thin-walled, non-elastic tubes by which it is returned to the heart. Thus the general scheme of the circulation is simple: the arteries spring from the heart, or from arteries of a higher order, and end in capillaries; the veins begin in capillaries and end in vessels of a higher order or in the heart. Actually, however, the system is complicated (*a*) by the interposition of the gills in the course of the outgoing current, as a result of which we have arteries serving as both afferent and efferent vessels of the respiratory capillaries, the efferent arteries taking their origin in those capillaries after the manner of veins; and (*b*) by the interposition of two important blood-purifying organs, the liver and the kidney, in the course of the returning current, as a result of which we have veins acting

as both afferent and efferent vessels of the hepatic and renal capillaries, the afferent vessels of both organs ending in capillaries after the fashion of arteries.

In the embryos of the higher, or air-breathing, Craniata the circulatory organs agree in essentials with the above description, the most important difference being that, as no gills are present, the branches of the ventral aorta do not break up into capillaries, but pass directly into the dorsal aorta, forming the *aortic arches* (Fig. 729, *Ab.*). With the appearance of the lungs, however, a very fundamental change occurs in the blood-system. The last aortic arch of each side give off a *pulmonary artery* (Fig. 730, *Ap.*) to the corresponding lung, and the blood, after circulating through the capillaries of that organ, is returned by a *pulmonary vein* (*lv.*), not into an ordinary systemic vein of higher order, but into the heart directly: there it enters the left side of the auricle, in which a vertical partition is developed, separating a *left auricle* (A^1), which receives the aërated blood from the lungs, from a *right auricle* (A), into which is poured the impure blood of the sinus venosus. Lastly, in Crocodiles, Birds, and Mammals the ventricle also becomes divided into right and left chambers (B.), and we get a four-chambered heart, having right and left auricles, and right and left ventricles: at the same time the sinus venosus ceases to exist as a distinct chamber. The left auricle receives aërated blood from the lungs and passes it into the left ventricle, whence it propelled

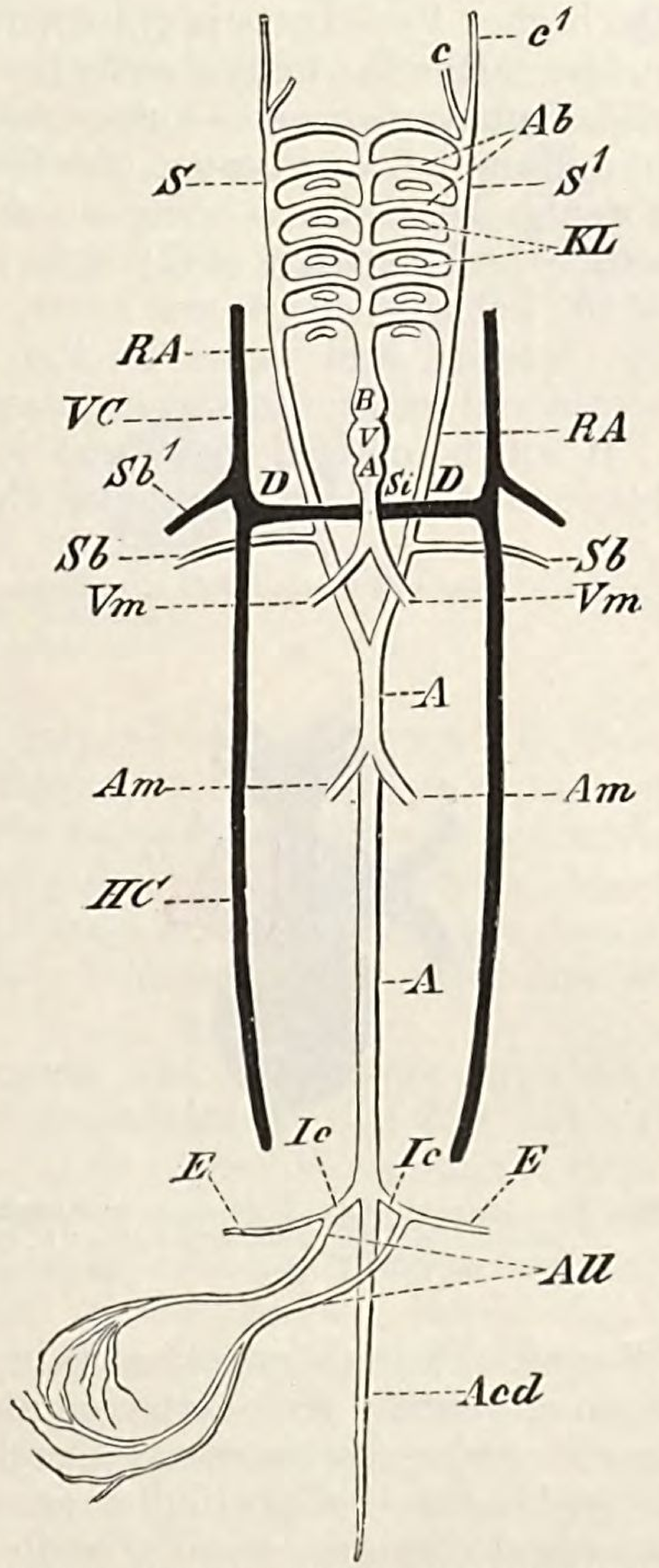


FIG. 729.—Diagram of the vascular system in the embryo of an **air-breathing Craniate**. *A*, dorsal aorta and auricle; *Ab*, aortic arches; *Acd*, caudal artery; *All*. allantoic arteries; *Am*, vitelline arteries; *B*, ventral aorta; *C*, C^1, carotid arteries; *D*, pre-caval veins; *Ic*, *E*, iliac arteries; *HC*, cardinal veins; *KL*, gill-clefts; *R. A.* *S*, S^1, roots of dorsal aorta; *Sb*, sub-clavian arteries; Sb^1, sub-clavian veins; *V*. Ventricle; *VC*, jugular vein; *Vm*, vitelline veins. (From Wiedersheim's *Vertebrata*.)

through the system: the right auricle receives impure blood from the system, and passes it into the right ventricle to be pumped into the lungs for aëration. Thus the four-chambered heart of the higher Vertebrata is quite a different thing from that of a Fish: in the latter the four chambers—sinus venosus, auricle, ventricle, and conus arteriosus—form a single longitudinal series, whereas in a Mammal, for instance, the four chambers constitute practically a double heart, there being no direct communication between the auricle and ventricle of the right side, or *respiratory heart*, and those of the left side, or *systemic heart*. The modifications undergone by the arteries and veins in the higher Vertebrata will be best considered under the various classes.

It will be noticed that there is a sort of rough correspondence between the blood-vessels of Craniata and those of the higher

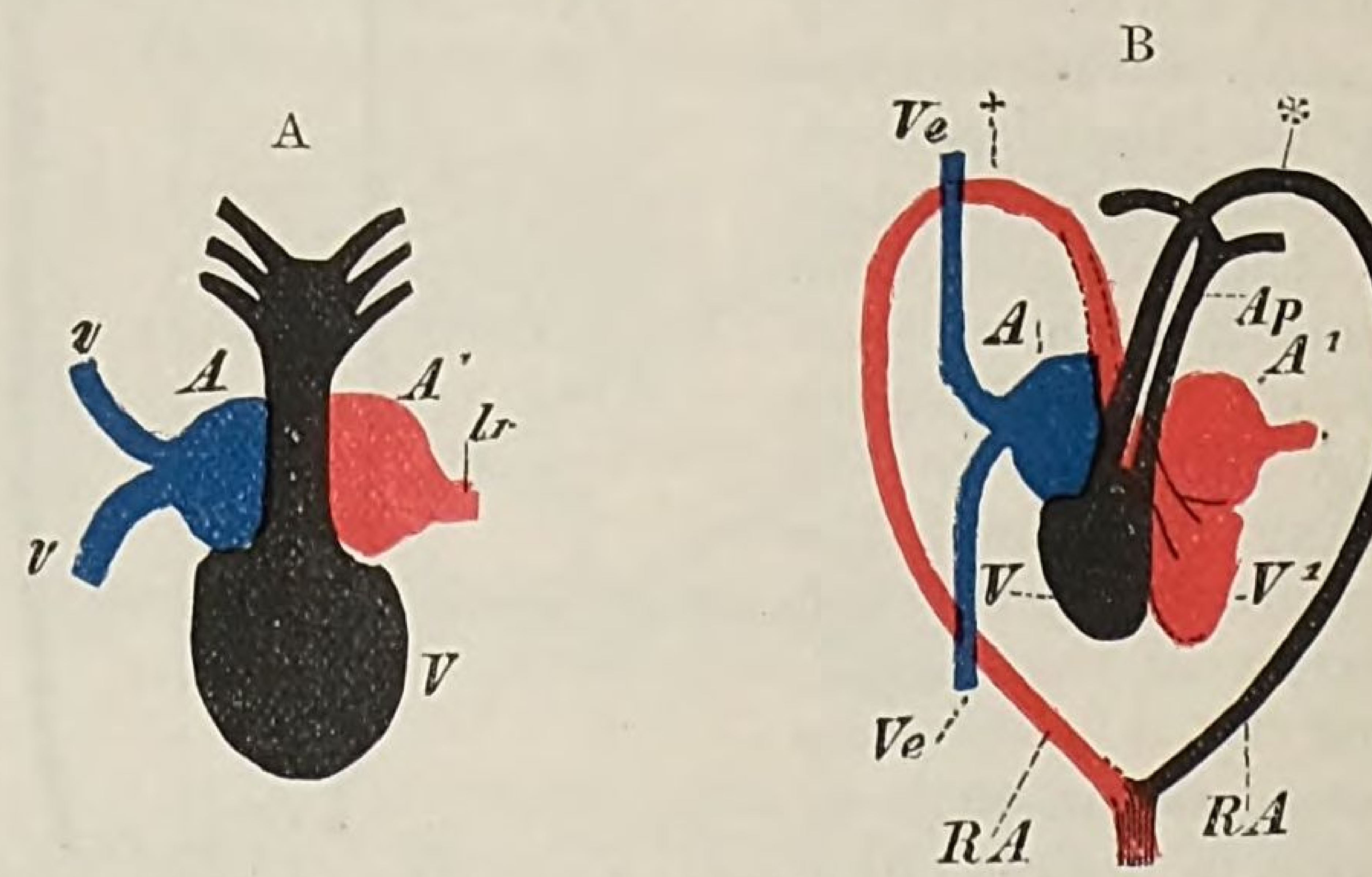


FIG. 730.—Diagram of the heart A, in an **Amphibian**; B, in a **Crocodile**. *A*, right auricle; *A'*, left auricle; *Ap*, pulmonary artery; *lr*, pulmonary vein; *RA*, aortic arches; *V*, ventricle; *V'*, left ventricle; *V*, *V*, and *Ve*, *Ve*, pre- and post-cavals. (From Wiedersheim's *Vertebrata*.)

Worms. The sub-intestinal vein, heart and ventral aorta together form a ventral vessel, the dorsal aorta a dorsal vessel, and the aortic arches commissural vessels. The heart is therefore to be looked upon as a portion of an original ventral vessel, which has acquired strongly muscular walls, and performs the whole function of propelling the blood. There seems to be some reason for thinking that the caudal, hepatic-portal, and hepatic veins represent detached portions of the original ventral vessel, while the lateral veins may be compared with the lateral vessels of some Annulates.

The *blood* of Craniata is always red, and is specially distinguished by the fact that the hæmoglobin to which it owes its colour is not dissolved in the plasma as in most red-blooded Invertebrates, but is confined to certain cells called *red blood corpuscles* (Fig. 731), which occur floating in the plasma in addition to, and in far greater numbers than, the leucocytes. They usually have

the form of flat oval discs (A.), the centre bulged out by a large nucleus (*nu.*), but in mammals (B.) they are bi-concave, non-nucleated and usually circular. They do not perform amœboid movements.

The colour of the blood varies with the amount of oxygen taken up by the hæmoglobin. When thoroughly aërated it is of a bright scarlet colour, but assumes a bluish-purple hue after giving up its oxygen to the tissues. Owing to the fact that oxygenated blood is usually found in arteries, it is often spoken of as *arterial*



FIG. 731.—Surface and edge views of red-blood corpuscles of Frog (A) and Man (B). *nu.* nucleus. (From Parker's *Biology*.)

blood, while the non-oxygenated, purple blood, being usually found in veins, is called *venous*. But it must not be forgotten that an artery, *e.g.*, the ventral aorta or the pulmonary artery, may contain venous blood, and a vein, *e.g.*, the pulmonary vein, arterial blood. The distinction between the two classes of vessels does not depend upon their contents, but upon their relations to the heart and the capillaries.

In addition to the blood-vessels the circulatory system of Craniata contains *lymph-vessels* or **lymphatics** (Fig. 728, *ly.*). In most of the tissues there is a network of *lymph-capillaries*, interwoven with, but quite independent of, the blood-capillaries. From this network lymphatic vessels pass off, and finally discharge their contents into one or other of the veins. Many of the lower Craniata possess spacious *lymph-sinuses* surrounding the blood-vessels, and there are communications between the lymphatics and the cœlome by means of minute apertures or *stomata*. The lymphatics contain a fluid called *lymph*, which is to all intents and purposes blood *minus* its red corpuscles. The lymph-plasma consists of the drainage from the tissues: it makes its way into the lymph capillaries, and thence into the lymphatics, which are all efferent vessels, conveying the fluid from the capillaries to the veins. Leucocytes are added to the plasma in bodies, called *lymphatic glands*, which occur in the course of the vessels. Valves may be present to prevent any flow of lymph towards the capillaries, and in some cases the course of the fluid is assisted by *lymph hearts*, muscular dilatations in the course of certain of the vessels. The lymphatics of the intestine have an important function in the absorption of fats, and are known as *lacteals* (*lc.*)

The **nervous system** attains a complexity, both anatomical and histological, unknown in the rest of the animal kingdom. It arises, as in other Chordata, from a dorsal *medullary groove* the edges of which unite and enclose a tube. From the ectoderm lining the tube the whole central nervous system, or *neuron*, is formed, its lumen forms the *neurocœle* or characteristic axial cavity of the neuron. So far the agreement with the lower Chordata is complete, but a fundamental advance is seen in the fact that at an early period—before the closure of the medullary groove—the anterior end of the neuron undergoes a marked dilatation and forms the rudiment of the *brain*, the rest becomimg the *spinal cord.* Moreover, as growth goes on a space appears in the mesoderm immediately surrounding the nervous system, and forms the *neural* or *cerebro-spinal cavity* already referred to (Fig. 715, *cs. c.*), so that the neuron, instead of being solidly imbedded in mesoderm, lies in a well-marked and often spacious tube enclosed by the neural arches of the vertebræ, and in front by the cranium (Fig. 715, B–D).

The *spinal cord* (Fig. 732) is a thick-walled cylinder, continuous in front with the brain. It is transversed from end to end by a narrow *central canal* (*3*), lined by ciliated epithelium derived from the superficial layer of in-turned ectoderm cells, the substance of the cord itself being formed from the deeper layers. The dorsal surface of the cord is marked by a deep, narrow, longitudinal groove, the *dorsal fissure* (*2*), the ventral surface is similarly scored by a *ventral fissure* (*1*); owing to the presence of these fissures a transverse section presents two almost semicircular halves with their straight edges applied to one another and joined in the middle by a narrow bridge (*4*, *5*) in which the central canal lies.

The cord is made up of two kinds of tissue. Surrounding the central canal and having a somewhat butterfly-shaped transverse section, is the *grey matter* (*a*, *e*) consisting of delicate, inter-twined, non-medullated nerve-fibres, amongst which are numerous nerve-cells. The superficial portion is composed of medullated nerve-fibres running longitudinally, and is called the *white matter* (*6*, *7*, *8*). In both grey and white matter the nervous elements are supported by a non-nervous tissue called *neuroglia*, formed of branched cells.

From the cord the *spinal nerves* are given off. They arise in pairs from the sides of the cord, and agree in number with the myomeres. Each nerve arises from the cord by two *roots*, a dorsal and a ventral. The *dorsal root* (Fig. 734, *d. r.*) is distinguished by the presence of a ganglion (*gn. d.r.*) containing nerve-cells, and its fibres are usually wholly afferent, conveying impulses from the various parts and organs of the body to the central nervous system; the *ventral root* (*v. r.*) is not ganglionated, and its fibres are efferent, conveying impulses from the neuron

outwards. Each root arises from one of the horns of the grey matter, and the two mingle to form the *trunk* (*sp.* 1–3) of the nerve, which emerges from the spinal canal usually between the arches of adjacent vertebræ. Soon after its emergence it divides into two chief divisions, the *dorsal* (*d.*) and *ventral* (*sp.* 1, &c.) *nerves.* The spinal nerves supply the muscles and skin of the trunk and limbs, and are therefore spoken of as *somatic nerves.*

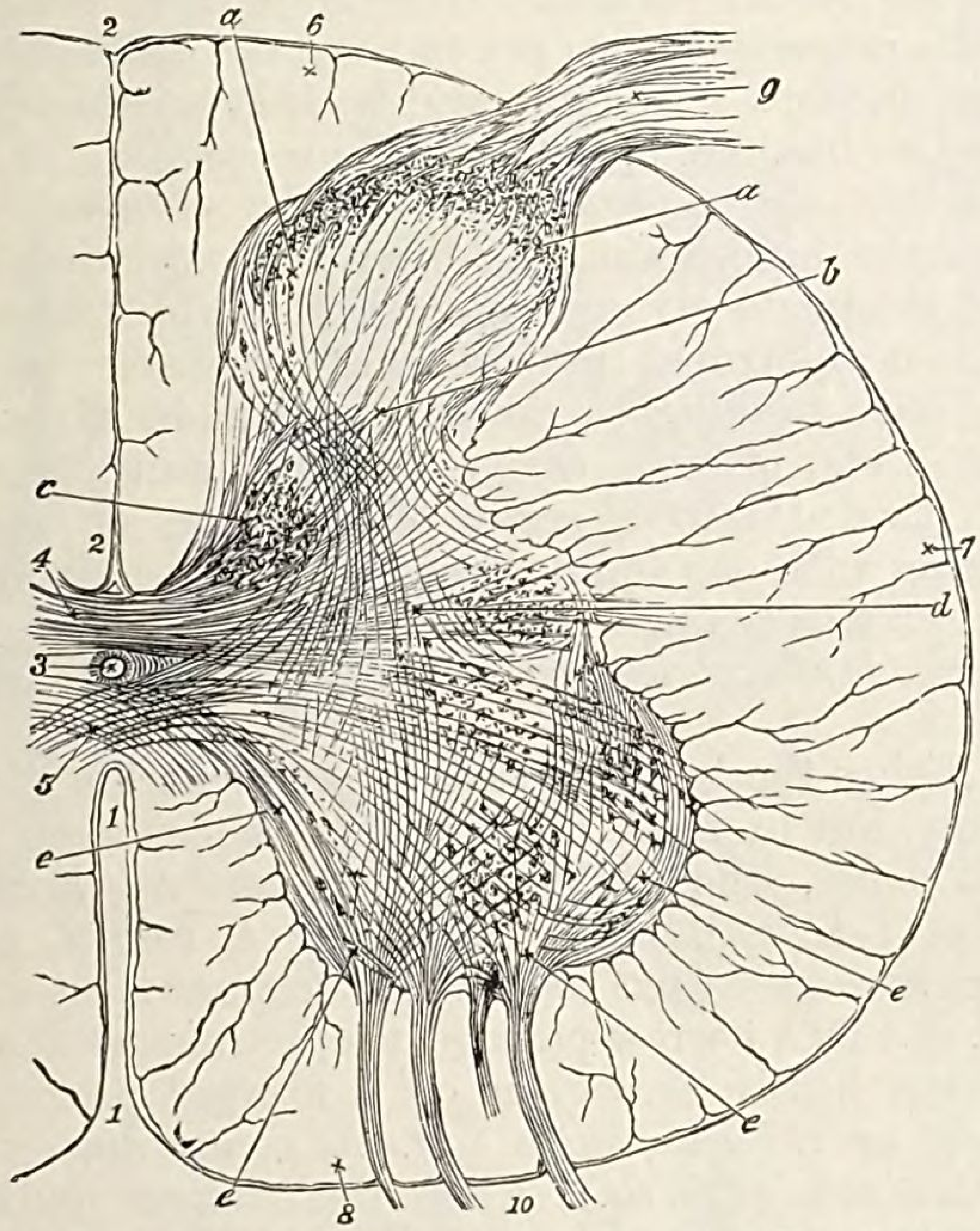


FIG. 732.—Transverse section of spinal cord. 1, ventral fissure; 2, dorsal fissure; 3, central canal; 4, 5, bridges connecting grey matter of right and left sides; 6, 7, 8, white matter; 9, dorsal root of spinal nerve; 10, ventral root. *a*, *b*, dorsal horn of grey matter; *c*, Clarke's column; *e*. ventral horn. (From Huxley's *Physiology*.)

Frequently groups of nerves unite with one another to form more or less complex networks called *plexuses.*

Closely associated with the spinal are the *sympathetic nerves* (Fig. 734, *sym*). They take the form of paired longitudinal cords, with ganglia (*sym. gn.*) at intervals, lying one on each side of the aorta in the dorsal wall of the cœlome. They contain both afferent and efferent fibres, the afferent derived from the dorsal, the efferent from the ventral roots of the spinal nerves, and both traceable, through those roots, into the grey matter of the cord. The sympathatic nerves supply the enteric canal and its glands, the heart, blood-vessels, &c., and are therefore denominated *splanchnic nerves.*

As already mentioned, the anterior end of the nervous system undergoes, at a very early period, a marked dilatation, and is distinguished as the *brain* (Fig. 733). Constrictions appear in the dilated part and divide it into three bulb-like swellings or vesicles, the fore-brain (A, *f. b.*), mid-brain (*m. b.*) and hind-brain (*h. b.*). Soon a hollow outpushing grows forwards from the first vesicle (B, *prsen*), and the third gives off a similar hollow outgrowth (*cblm.*) from its dorsal surface. The brain now consists of five divisions: the *prosencephalon* (*prs. cn.*) and the *diencephalon* (*dien.*), derived from the fore-brain: the *mid-brain* or *mesencephalon* (*m. b.*) which remains unaltered: and the *epencephalon*, or *cerebellum* (*cblm.*), and the *metencephalon*, or *medulla oblongata* (*med. obl.*) derived from the hind-brain. Additional constrictions appear in the medulla oblongata giving it a segmented appearance, but they disappear as development proceeds, and, whatever may be their significance, have nothing to do with the main divisions of the adult organ. The original cavity of the brain becomes correspondingly divided into a series of chambers or *ventricles*, all communicating with one another and called respectively the *fore-ventricle* or *prosocœle*, *third ventricle* or *diacœle*, *mid-ventricle* or *mesocœle*, *cerebellar ventricle* or *epicœle*, and *fourth ventricle* or *metacœle*.

In some Fishes the brain consists throughout life of these five divisions only, but in most cases the prosencephalon grows out into paired lobes, the right and left *cerebral hemispheres* or *parencephala* (I–L, *c.h*), each containing a cavity, the *lateral ventricle* or *paracœle* (*pa. cœ*) which communicates with the diacœle (*di. cœ.*) by a narrow passage, the *foramen of Monro* (*f. m.*). Moreover, each hemisphere gives off a forward prolongation, the *olfactory lobe* or *rhinencephalon* (*olf. l.*), containing an *olfactory ventricle* or *rhinocœle* (*rh. cœ.*): when there is an undivided prosencephalon the olfactory lobes (C, D, *olf. l.*) spring from it. In the embryo of some forms there is a median *unpaired olfactory lobe*, like that of Amphioxus.

The brain undergoes further complications by the unequal thickening of its walls. In the medulla oblongata the floor becomes greatly thickened (D, H, K.), while the roof remains thin, consisting of a single layer of epithelial cells, assuming the character therefore of a purely non-nervous epithelial layer (*ependyme*). In the cerebellum the thickening takes place to such an extent that the epicœle is usually obliterated altogether. In the mid-brain the ventral wall is thickened in the form of two longitudinal bands, the *crura cerebri* (*cr. crb.*), the dorsal wall in the form of paired oval swellings, the *optic lobes* (*opt. l.*): extensions of the mesocœle into the latter form the *optic ventricles* or *optocœles* (G. *opt. cœ.*): the median portion of the mesocœle is then called the *iter* (*I*) or *aqueduct of Sylvius*. In the diencephalon the sides

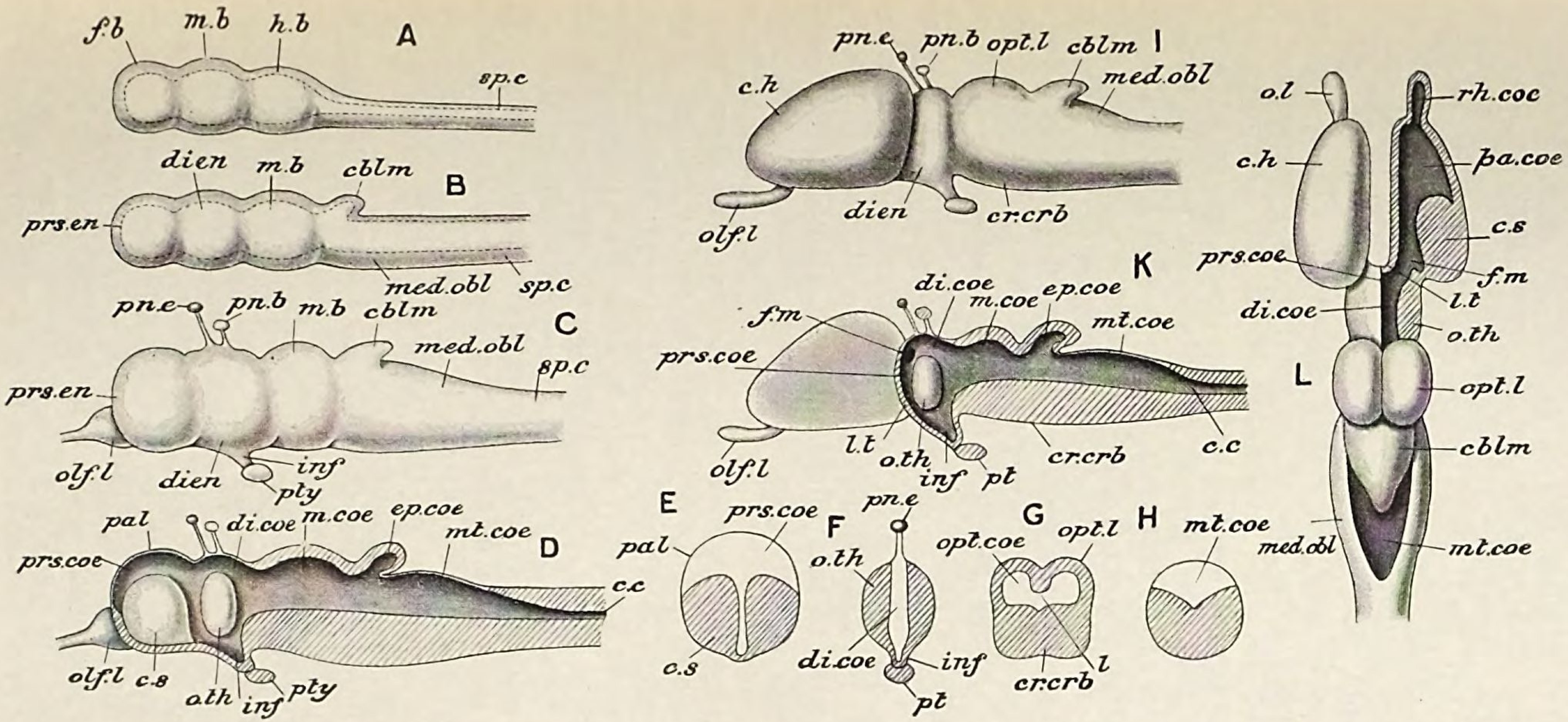


FIG. 733.—Diagrams of the **Craniate brain**. A, first stage, side view, the cavity indicated by a dotted line; B, second stage; C, side view of fully-formed brain with undivided prosencephalon; D, the same in sagittal section; E, transverse section of prosencephalon; F, of diencephalon; G, of mesencephalon; H, of metencephalon; I, side view of brain with cerebral hemispheres; K, sagittal section of the same; L, dorsal view, the cavities exposed on the right side. *cblm.* cerebellum; *c. c.* central canal; *cr. crb.* crura cerebri; *c. h.* cerebral hemispheres; *c. s.* corpora striata; *di. cœ.* diacœle or third ventricle; *dien.* diencephalon; *ep. cœ.* epicœle; *f. b.* fore-brain; *f. m.* foramen of Monro; *h. b.* hind-brain; *l.* iter; *inf.* infundibulum; *l. t.* lamina terminalis; *m. b.* mid-brain; *m. cœ.* mesocœle; *med. obl.* medulla oblongata; *mt. cœ.* metacœle or fourth ventricle; *olf. l.* olfactory lobes; *opt. cœ.* optocœles; *opt. l.* optic lobes; *o. th.* optic thalami; *pa. cœ.* paracœles or lateral ventricles; *pal.* pallium; *pn. b.* pineal body; *pn. e.* pineal sense-organ; *prs. cœ.* prosocœle; *prsen.* prosencephalon; *pty.* pituitary body; *rh. cœ.* rhinocœles; *sp. c.* spinal cord.

become thickened forming paired masses, the *optic thalami* (D, F, L, *o. th.*), the roof remains for the most part in the condition of a thin membrane (*ependyme*) composed of a single layer of cells, but part of it gives rise to a very peculiar adjunct of the brain, the *pineal apparatus.* This originates as a narrow hollow outgrowth, the *epiphysis.* The epiphysis is frequently double, one portion being in front of the other, and the two parts may be widely separated. From this, or when it is double, from one of its portions, a diverticulum is developed, which becomes constricted off in the Lampreys and some Reptiles to form an eye-like body, the *pineal eye* (*pn.e.*); sometimes a second, less fully formed *parapineal eye* may be formed from another part of the epiphysis. In most adult Vertebrates the epiphysis is represented by a gland-like structure, the *pineal body* (*pn. b.*), connected with the roof of the diencephalon by a hollow or solid stalk. The term *paraphysis* is sometimes applied to an outgrowth of the roof of the fore-brain developed in front of the epiphysis in the hinder region of the prosencephalon. The floor of the diencephalon grows downwards into a funnel-like prolongation, the *infundibulum* (*inf.*): with this the pituitary diverticulum of the pharynx (p. 81) comes into relation, and there is formed, partly from the dilated end of the diverticulum, partly from the extremity of the infundibulum, a gland-like structure, the *pituitary body* or *hypophysis* (*pt.*) always situated immediately in front of the anterior extremity of the notochord and between the diverging posterior ends of the trabeculæ. In cases where cerebral hemispheres are not developed, the roof or *pallium* of the undivided fore-brain is reduced to a layer of epithelium (D and E. *pal.*): its floor is thickened so as to form large paired masses, the *corpora striata* (*c. s.*). When hemispheres are developed the corpora striata form the floors of the two lateral ventricles (L. *c. s.*), and the roof (pallium) of each is formed of nervous tissue. In such cases the front wall of the diencephalon remains very thin, and is distinguished as the *lamina terminalis* (*l. t.*): this is the actual anterior extremity of the central nervous system, the cerebral hemispheres being lateral outgrowths.

In the preceding description the brain has been described as if its parts were in one horizontal plane, but, as a matter of fact, at a very early period of development the anterior part becomes bent down over the end of the notochord, so that the whole organ assumes a retort-shape, the axis of the fore-brain being strongly inclined to that of the hind-brain. The bend is known as the *cerebral flexure*: it is really permanent, but, as the hemispheres grow forward parallel to the hind-brain and the floor of the mid- and hind-brain thickens, it becomes obscure, and is not noticeable in the adult.

The brain, like the spinal cord, is composed of grey and white matter, but the grey matter either forms a thin superficial layer

or *cortex*, as in the hemispheres and cerebellum, or occurs as ganglionic masses surrounded by white matter.

The whole cerebro-spinal cavity is lined with a tough membrane, the *dura mater*, and both brain and spinal cord are covered by a more delicate investment, the *pia mater:* the space between the two contains a serous fluid. In the higher forms there is a delicate *arachnoid membrane* outside the pia, and in many cases the regions of the pia in immediate contact with the thin epithelial roofs of the diencephalon and medulla become greatly thickened and very vascular, forming in each case what is known as a *choroid plexus.*

From the brain are given off *cerebral* or *cranial nerves:* these, like the spinal nerves, are paired, but, unlike them, are strictly limited in number, the number being constant, at least within very narrow limits: there are ten pairs in Fishes and Amphibians, twelve in Reptiles, Birds, and Mammals.

The *first* or *olfactory nerve* (Fig. 734, I.) is rather a bundle of fibres than a single nerve: it arises from the olfactory lobe, and supplies the organ of smell, *i.e.*, the epithelium of the olfactory sac (see below). It is therefore a purely sensory nerve.

The *second* or *optic nerve* (II.) arises from the ventral region of the diencephalon, just in front of the infundibulum. It differs from all the other nerves in being originally a hollow out-pushing of the brain, containing a prolongation of the diacœle (see Fig. 741). It supplies the retina or actual organ of sight, and is therefore a purely sensory nerve.

The *third* or *oculomotor nerve* (III.) arises from the crus cerebri or ventral region of the mid-brain. In its course is a ganglion, the *oculomotor* or *ciliary ganglion* (*c. gn.*). It supplies four out of the six muscles of the eye-ball (see below, Fig. 742), viz., the superior, inferior, and internal recti, and the inferior oblique (Fig. 742, III.), as well as the ciliary muscles and muscles of the iris in the interior of the eye. It is therefore a purely motor nerve.

The *fourth* or *trochlear nerve* (Figs. 734 and 742, IV.) arises from the dorsal surface of the brain at the junction of the mid-brain with the medulla oblongata. It is a very small and purely motor nerve, supplying only the superior oblique muscle of the eye.

The *fifth* or *trigeminal nerve* (Fig. 734, V.) is of great size and wide distribution. It arises from the side of the medulla, frequently by two roots, a dorsal and a ventral, thus resembling in its origin a spinal nerve. In some instances each root, or the dorsal root only, has a ganglion near its origin, in others the two roots enter a single *Gasserian ganglion* (*g. gn.*) The trunk of the nerve early divides into two principal branches, the *ophthalmic* and the *mandibular* (V. *md.*)*:* the latter sends off a *maxillary* nerve (V. *mx.*), and we thus get the three divisions to which the name trigeminal is due. The *ophthalmic nerve* frequently divides into

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two branches, a superficial (V. *o. s.* and a deep V. *o. p.*): it is purely sensory, and supplies the skin in the neighbourhood of the mouth and certain parts in the orbit. The *maxillary nerve* (V. *mx.*) is also sensory: it supplies the parts in relation with the upper jaw, including the teeth. The *mandibular nerve* (V. *md.*) is partly sensory, partly motor: it supplies the muscles of the jaws, the skin and teeth of the lower jaw, and sends off a *gustatory nerve* or nerve of taste to the epithelium of the tongue. The ophthalmic nerve is connected by a branch with the ciliary ganglion.

The *sixth* or *abducent* (Figs. 734 and 742, VI.) is a small motor nerve, arising from the ventral region of the medulla, and supplying the external rectus muscle of the eye. We thus have the remarkable fact that out of ten, or at the most twelve, cerebral

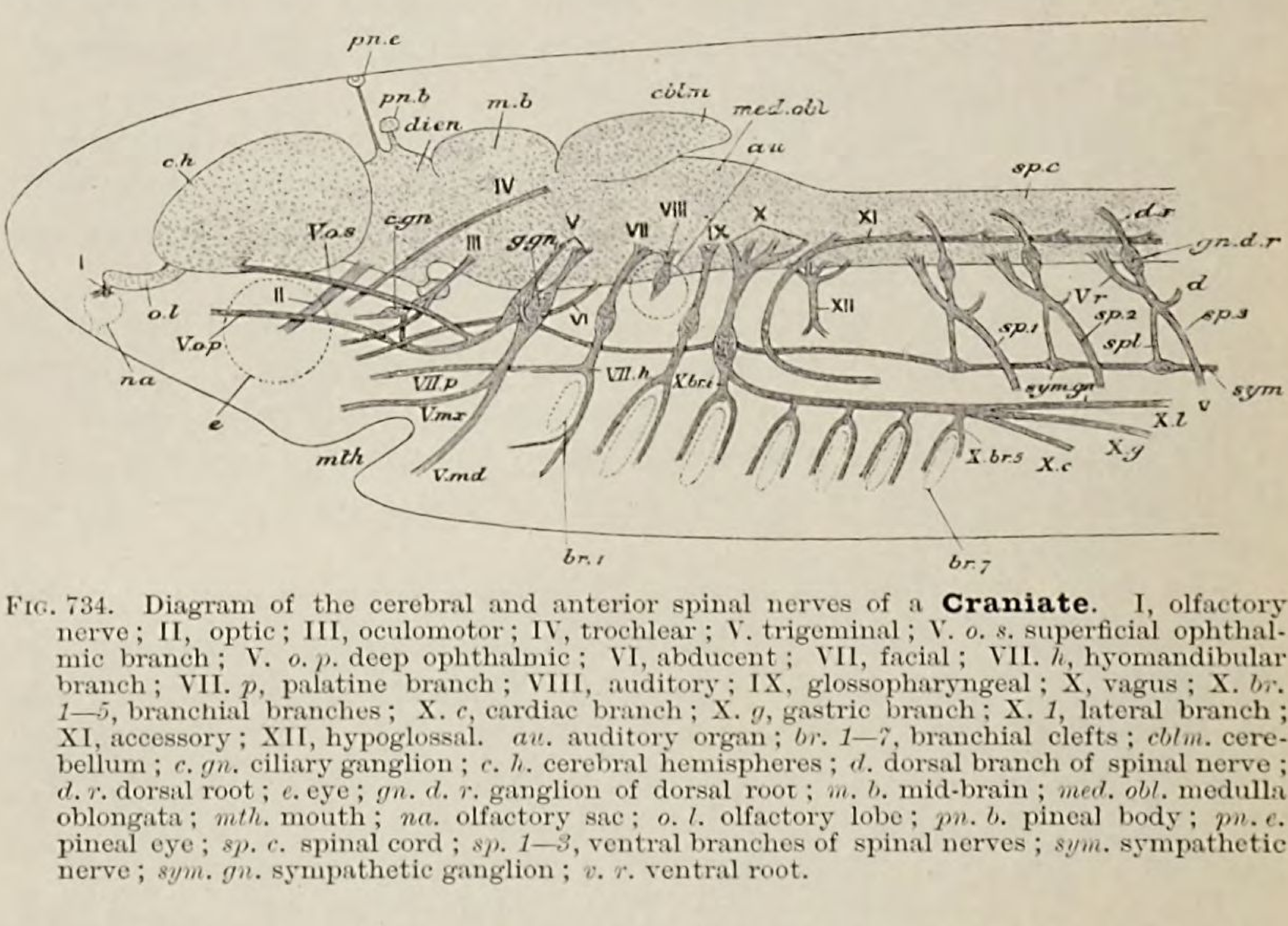


FIG. 734. Diagram of the cerebral and anterior spinal nerves of a **Craniate**. I, olfactory nerve; II, optic; III, oculomotor; IV, trochlear; V. trigeminal; V. *o. s.* superficial ophthalmic branch; V. *o. p.* deep ophthalmic; VI, abducent; VII, facial; VII. *h*, hyomandibular branch; VII. *p*, palatine branch; VIII, auditory; IX, glossopharyngeal; X, vagus; X. *br. 1—5*, branchial branches; X. *c*, cardiac branch; X. *g*, gastric branch; X. *1*, lateral branch; XI, accessory; XII, hypoglossal. *au.* auditory organ; *br. 1—7*, branchial clefts; *cblm.* cerebellum; *c. gn.* ciliary ganglion; *c. h.* cerebral hemispheres; *d.* dorsal branch of spinal nerve; *d. r.* dorsal root; *e.* eye; *gn. d. r.* ganglion of dorsal root; *m. b.* mid-brain; *med. obl.* medulla oblongata; *mth.* mouth; *na.* olfactory sac; *o. l.* olfactory lobe; *pn. b.* pineal body; *pn. e.* pineal eye; *sp. c.* spinal cord; *sp. 1—3*, ventral branches of spinal nerves; *sym.* sympathetic nerve; *sym. gn.* sympathetic ganglion; *v. r.* ventral root.

nerves, three are devoted to the supply of the six small muscles by which the eye-ball is moved, and of those by which the accommodation of the eye for varying distances is effected.

The *seventh* or *facial* (Fig. 734, VII.) is, like the fifth, a mixed nerve in the lower Craniata, *i.e.*, contains both sensory and motor fibres. It arises from the side of the medulla, a short distance behind the fifth, and is dilated near its origin into a *facial ganglion*. It has two chief branches, a *palatine* (VII. *p.*), which passes in front of the mandibulo-hyoid gill-cleft, and supplies the mucous membrane of the palate, and a *hyomandibular* (VII. *h.*), which passes behind the same cleft and sends branches to the lower jaw, and to the hyoid arch. In aquatic Vertebrata an *ophthalmic* branch is given off from the trunk of the nerve, and usually

accompanies the ophthalmic division of the fifth. In the higher Vertebrata the seventh becomes a purely motor nerve, supplying the muscles of the face.

The *eighth* or *auditory nerve* (VIII.) arises immediately behind the seventh, with which it is intimately connected at its origin. It is a purely sensory nerve, supplying the organ of hearing, *i.e.*, the epithelium of the membranous labyrinth presently to be described.

The *ninth* or *glossopharyngeal* (IX.) is a mixed nerve: it arises from the lateral region of the medulla, behind the organ of hearing, and is connected at its origin with the vagus ganglion (see below). Its trunk passes downwards and forks over the second gill-cleft, sending an anterior branch to the hyoid arch which bounds the cleft in front, and a posterior branch to the first branchial arch which bounds it posteriorly. Thus the entire nerve supplies the second gill-pouch, including both branchial filaments and muscles: its anterior branch goes to the posterior hemibranch of the hyoid arch, its posterior branch to the anterior hemibranch of the first branchial arch. In the air-breathing Vertebrata, in which gills are absent, the glossopharyngeal sends a *gustatory nerve* to the tongue and supplies the pharynx.

The *tenth nerve* (X.), called the *vagus* or *pneumogastric*, is distinguished by its wide distribution. It arises by numerous roots from the side of the medulla, the roots uniting into a stout trunk with a *vagus ganglion* at its origin. From the trunk are given off, in the first place, *branchial nerves* (X. *br.* 1–5), corresponding in number and position to the gill-slits from the third to the last inclusive. Each branchial nerve behaves in exactly the same way as the glossopharyngeal; it forks over the gill-pouch to which it belongs, sending one branch to the anterior, another to the posterior wall of the pouch. Thus each *gill-pouch* has its own nerve while each *gill* receives its supply from two sources; for instance, the gill of the second branchial arch has its anterior hemibranch innervated from the first, its posterior hemibranch from the second branchial branch of the vagus. The vagus also gives off a *cardiac nerve* (X. *c*) to the heart, a *gastric nerve* (X. *g*) to the stomach, and a *lateral nerve* (X. *l*) which passes backwards along the side of the body and supplies the cutaneous sense-organs (see below). In the air-breathing Craniata there are, of course, no branchial nerves; but the vagus still retains control of the respiratory organs by giving origin to *pulmonary nerves* to the lungs and *laryngeal nerves* to the larynx.

The above mentioned ten nerves are all that exist in most of the lower Craniata: the *eleventh* or *accessory nerve* (XI.) appears first in Reptiles. It arises by numerous roots from the anterior part of the spinal cord, passes forward, between the dorsal and ventral roots of the spinal nerves, and finally leaves the medulla just behind the vagus. It is thus a spinal nerve as regards its origin,

a cerebral nerve as regards its final exit. It is purely motor supplying certain of the muscles of the shoulder.

The *twelfth* or *hypoglossal* (XII.) arises from the ventral aspect of the medulla oblongata, after the manner of the ventral root of a spinal nerve. It is purely motor, and supplies the muscles of the tongue and certain neck-muscles. In the Amphibia its place is taken by the first spinal nerve, and there is no doubt that it is to be looked upon as a spinal nerve which has become included in the cranial region: even in some Fishes it passes out through the skull.

The sympathetic nerve (*sym.*) is continued into the head and becomes connected with some of the cerebral nerves.

It will be noticed that there are facts in connection with the cerebral nerves which suggest that they, like the spinal nerves, have a segmental value, and indicate that the head of a Vertebrate, like that of an Arthropod, is composed of fused metameres. For instance, the nerves to the gills have a regular segmental arrangement, and the conclusion is obvious that each visceral arch represents a metamere, the seventh, the ninth, and the branchial branches of the tenth being the corresponding segmental nerves. But it has been shown that at an early period of development the mesoderm of the head becomes divided into a number (9–19) of distinct segments, like those which give rise to the myomeres of the trunk and tail, and it is by no means certain that there is any precise correspondence between this original segmentation of the head and the segmentation of the pharynx which gives rise to the gills and associated structures. It has been stated that the first head-metamere gives rise to the superior, inferior, and internal rectus muscles of the eye, the second to the superior oblique, and the third to the external rectus. If this be so, the third, fourth, and sixth are true segmental nerves, and the anomalous fact of three out of ten nerves being devoted to the supply of the eye-muscles is satisfactorily explained. It seems tolerably certain that the third, fourth, sixth and twelfth nerves correspond to ventral roots of spinal nerves—they are all motor, and, except the fourth, arise from the ventral region of the brain: the fifth, with the exception of its motor root, and the seventh and eighth, ninth and tenth appear to correspond to dorsal roots.

Sensory Organs.—The whole surface of the body forms an organ of touch, but special tactile organs are more or less widely distributed. *End-buds* consist of ovoidal groups of sensory cells supplied by a special nerve: *touch-cells* (Fig. 735, A) are dermal nerve-cells occurring at the termination of a sensory nerve: *touch-corpuscles* (B) are formed of an ovoidal mass of connective tissue containing a ramified nerve, the terminal branches of which end in touch-cells: *Pacinian corpuscles* (C) consist of a terminal nerve-

branch surrounded by a complex laminated sheath. Touch-corpuscles and Pacinian bodies are found only in the higher forms.

In Fishes, characteristic sense-organs are present, known as the *organs of the lateral line*. Extending along the sides of the trunk

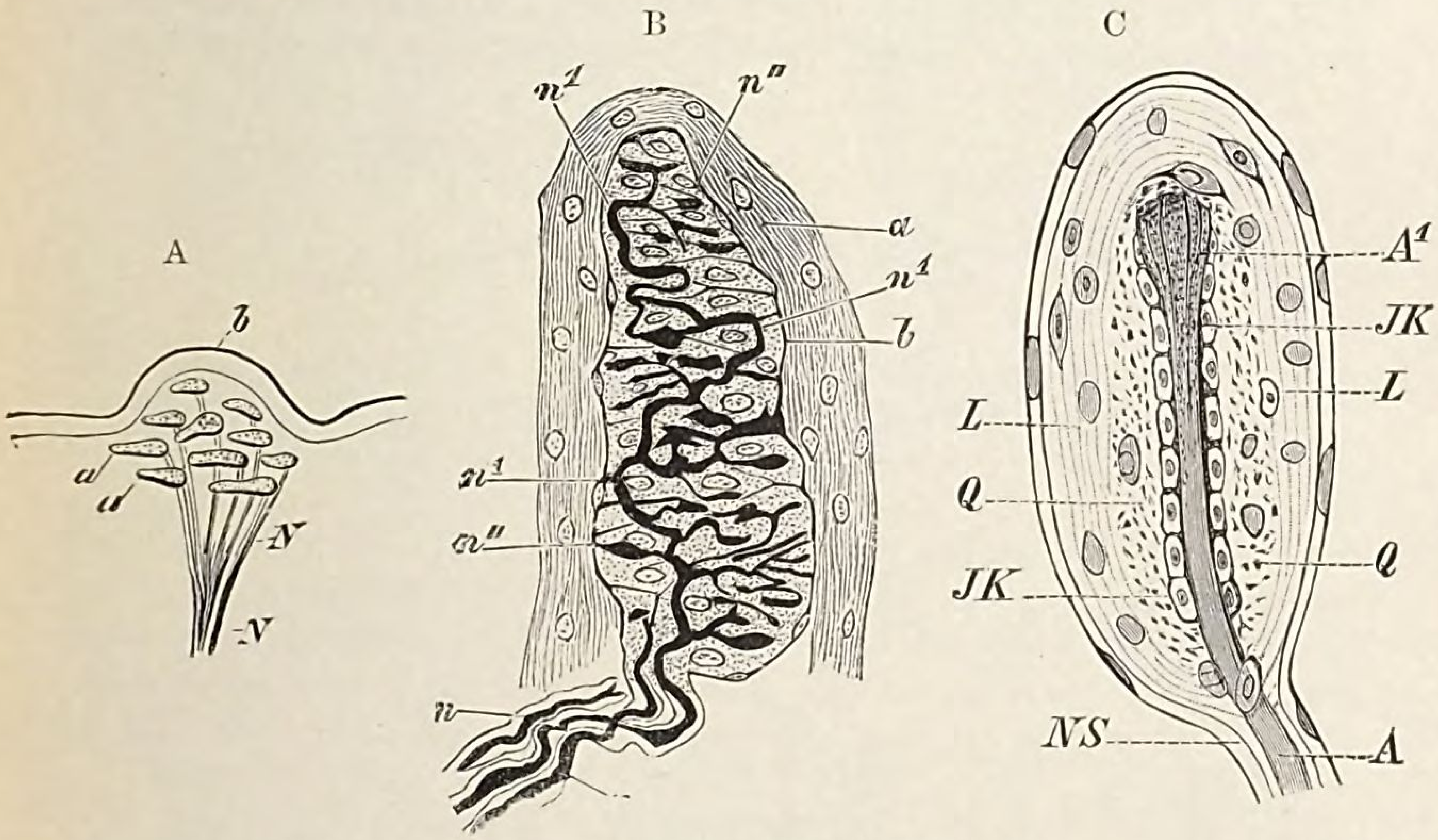


FIG. 735.—A, tactile spot from skin of **Frog**. *a*, touch-cells; *b*, epidermis; *N*, nerve. B, tactile corpuscle from dermal papilla of **human** hand. *a*, connective-tissue investment; *b*, touch-cells; *n*, *n′*, *n″*, *n‴*, nerve. C, Pacinian corpuscle from beak of **Duck**. *A*, *A′*, neuraxis; *JK*, central knob and surrounding cells; *L*, *Q*, investing layers; *NS*, medullary sheath of nerve. (From Wiedersheim's *Vertebrata*.)

and tail is a longitudinal streak, due to the presence either of an open groove or of a tube sunk in the epidermis, and continued on to the head in the form of branching grooves or canals (Fig. 736, A). The organs are lined with epithelium (B), some of the cells of which (*b*) have the rod-like form characteristic of sensory cells, and are produced at their free ends into hair-like processes (*c*): they are innervated by the lateral branch of the vagus, and, in the head, by the seventh and sometimes also the ninth nerve. At their first appearance in the embryo the organs of the lateral line are distinct, segmentally-arranged patches of sensory epithelium in intimate connection with the ganglia of the third, fifth, seventh, ninth, and tenth nerves. Cutaneous sense-organs, having at first a metameric arrangement, also occur in the aquatic Amphibia.

The sense of **taste** is lodged in the tongue, the epithelium of which contains end-buds (Fig. 737) similar to those of the skin and supplied by the gustatory branches of the trigeminal and glosso-pharyngeal.

The **olfactory organ** is typically a sac-like invagination of the skin of the snout, anterior to the mouth, and communicating with

the exterior by an aperture, the *external nostril.* It is paired in all Craniata, except Cyclostomes, in which there is a single olfactory sac, supplied, however, by paired olfactory nerves. The sac is lined by the olfactory mucous membrane or *Schneiderian membrane*, the epithelium of which contains peculiar, elongated sensory cells (Fig. 738), their free ends often produced into hair-like processes. In the Dipnoi and all higher groups the posterior end of each sac

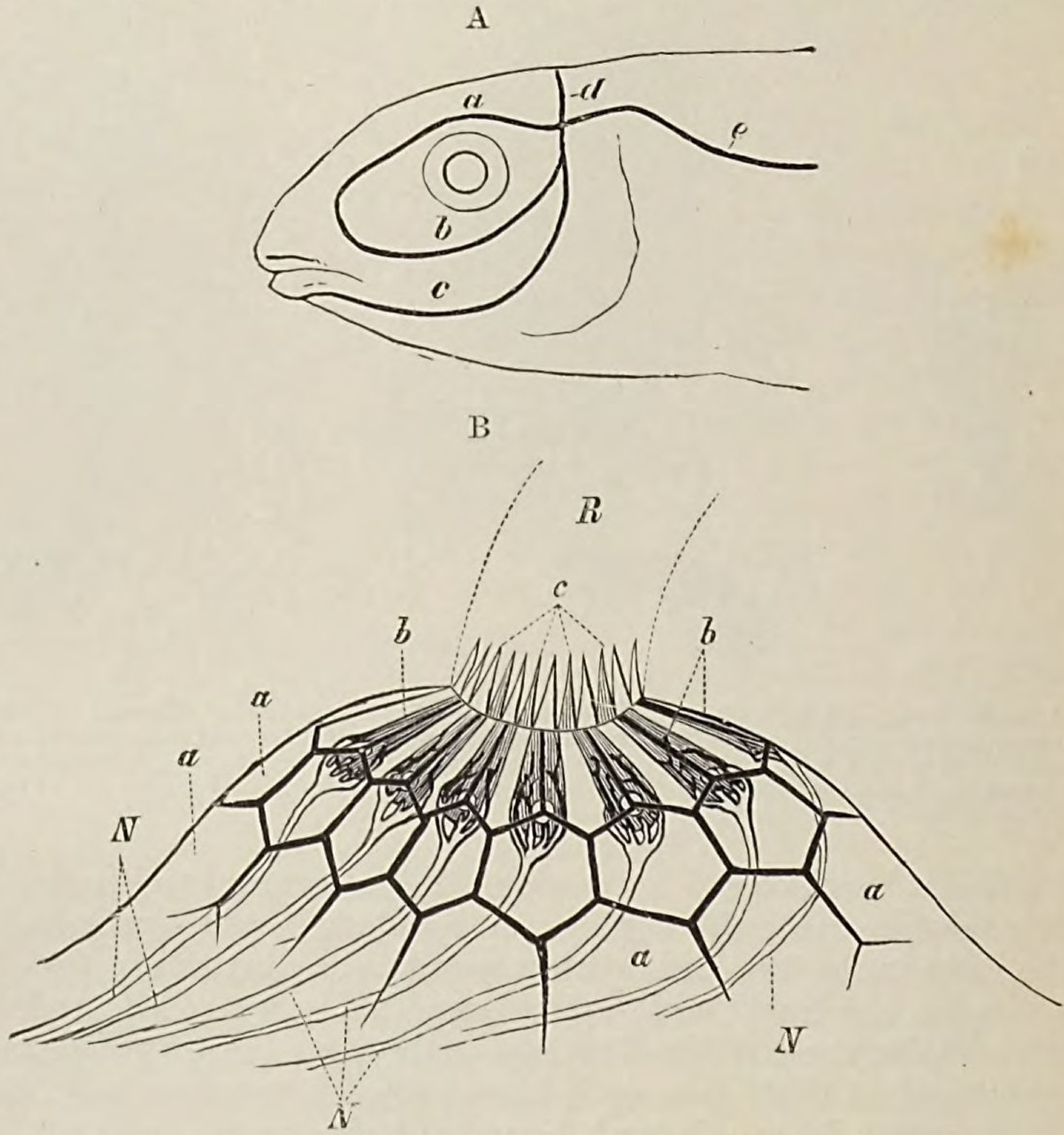


FIG. 736.—A, diagram of the organs of the lateral line in a **Fish**. *e*, lateral line; *a*—*d*, its continuation on the head. B, organ of the lateral line in a tailed **Amphibian** (semi-diagrammatic). *a*, epidermic cells, through which are seen *b*, sensory cells; *c*, sensory hairs; *N*, nerve; *R*, hyaline tube. (From Wiedersheim's *Vertebrata.*)

communicates with the cavity of the mouth by an aperture called the *posterior nostril*, and a similar communication occurs in the case of the unpaired organ of the Hags.

In many air-breathing Vertebrates there is formed an offshoot from the olfactory organ, which, becoming separated, forms a distinct sac lined with olfactory epithelium and opening into the mouth. This is *Jacobson's Organ:* it is supplied by the olfactory and trigeminal nerves.

The **paired eye** is a more or less globular structure, lying in

the orbit, and covered externally by a thick coat of cartilage or of dense fibrous tissue, the optic capsule or *sclerotic* (Fig. 739, *scl.*).

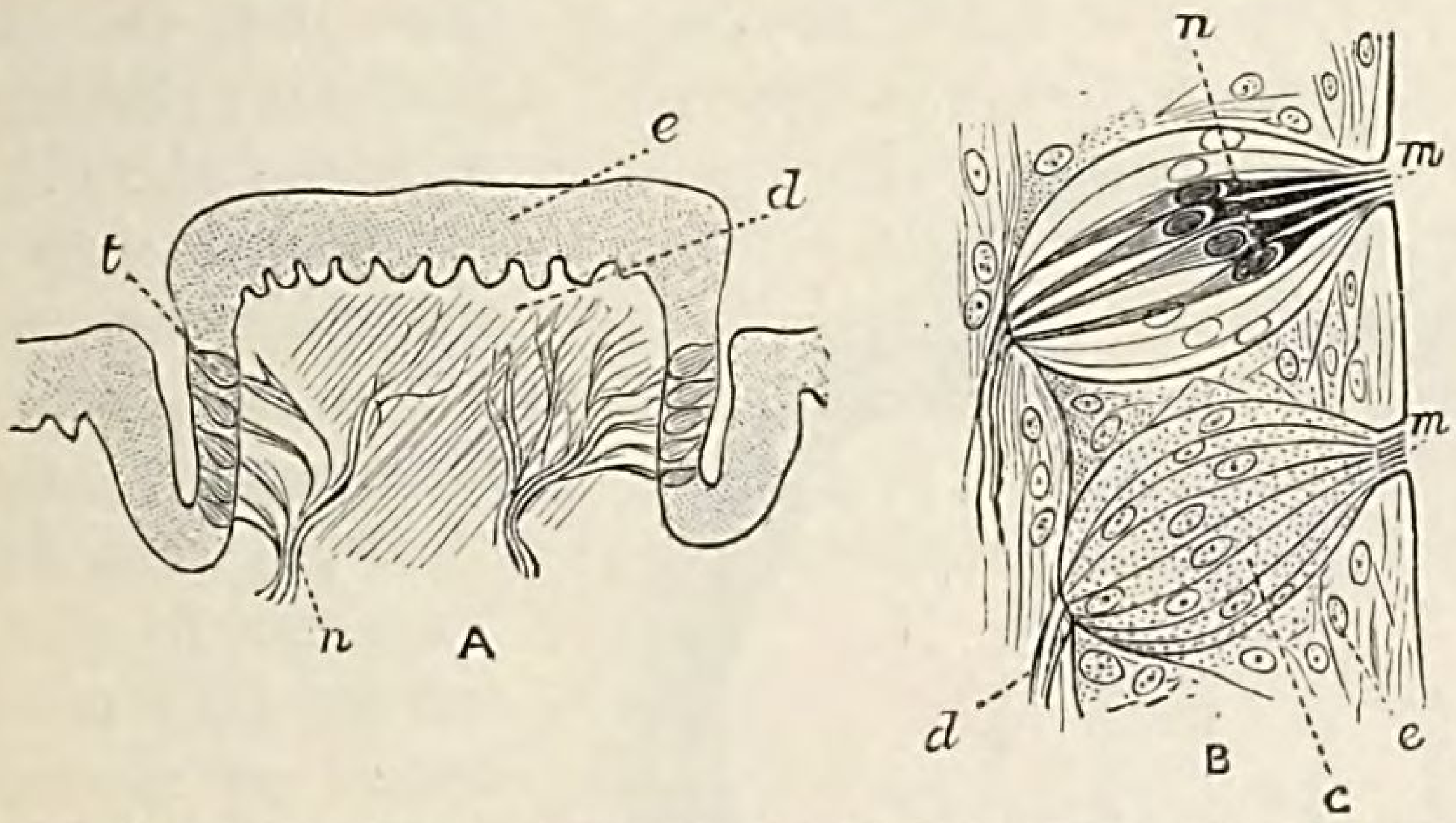


FIG. 737.—A, vertical section of one of the papillæ of the tongue of a **Mammal**. *d*, sub-mucosa; *e*. epithelium; *n*. nerve-fibres; *t*. taste-buds. B, two taste-buds. *c*. covering cells shown in lower bud; *d*, sub-mucosa; *e*. epithelium of tongue; *m*, sensory processes; *n*, internal sensory cells shown in upper bud. (From Foster and Shore's *Physiology*.)

On the outer or exposed portion of the eye the sclerotic is replaced by a transparent membrane, the *cornea* (*c.*), formed of a peculiar variety of connective tissue, and covered on both its outer and inner faces by a layer of epithelium. The curvature of the cornea is not the same as that of the sclerotic, so that the whole external coat of the eye has the character of an opaque spherical case—the sclerotic, having a circular hole cut in one side of it and fitted with a transparent window—the cornea. The latter is almost flat in Fishes, but bulges outwards in terrestrial Vertebrates.

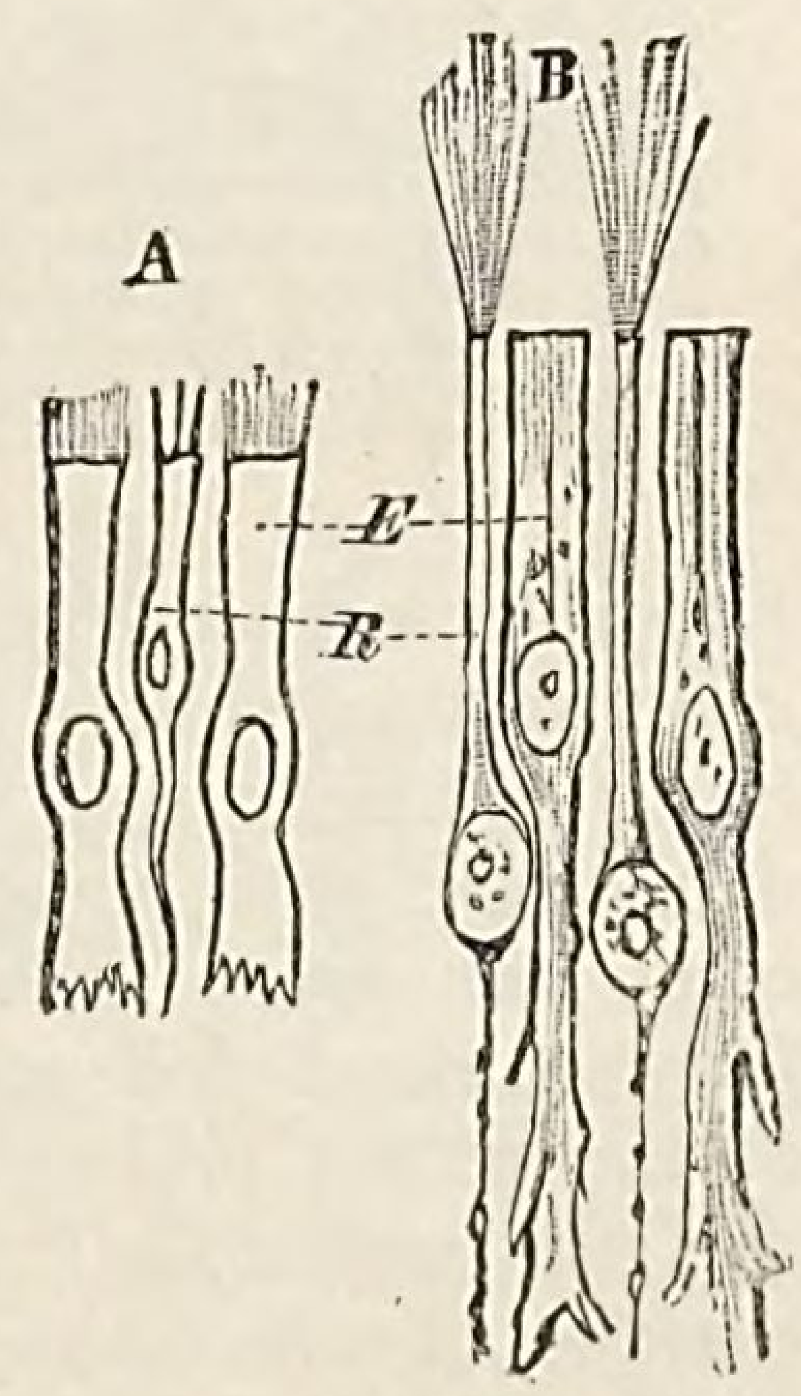


FIG. 738.—Epithelial cells of olfactory mucous membrane. A, of **Lamprey**; B, of **Salamander**. *E*, interstitial cells; *R*, olfactory cells. (From Wiedersheim's *Vertebrata*.)

Lining the sclerotic is the second coat of the eye—the *choroid* (*ch.*)—formed of connective tissue abundantly supplied with blood vessels. At the junction of sclerotic and cornea, it becomes continuous with a circular membrane (*I*), placed behind but at some distance from the cornea and called the *iris*. This latter is strongly pigmented, the colour of the pigment varying greatly in different species, and giving, as seen through the transparent cornea, the characteristic colour of the eye. The iris is perforated in the centre by a circular or slit-like aperture, the *pupil*, which, in the entire eye, appears like a black spot in the middle of the coloured portion. Except in Fishes, the pupil can be enlarged by the action of a set of radiating unstriped muscle-fibres con-

tained in the iris, and contracted by a set of circular fibres; and the anterior or outer portion of the choroid, where it joins the iris, is thrown into radiating folds, the *ciliary processes* (*C. P.*), containing unstriped muscular fibres, the *ciliary muscle*.

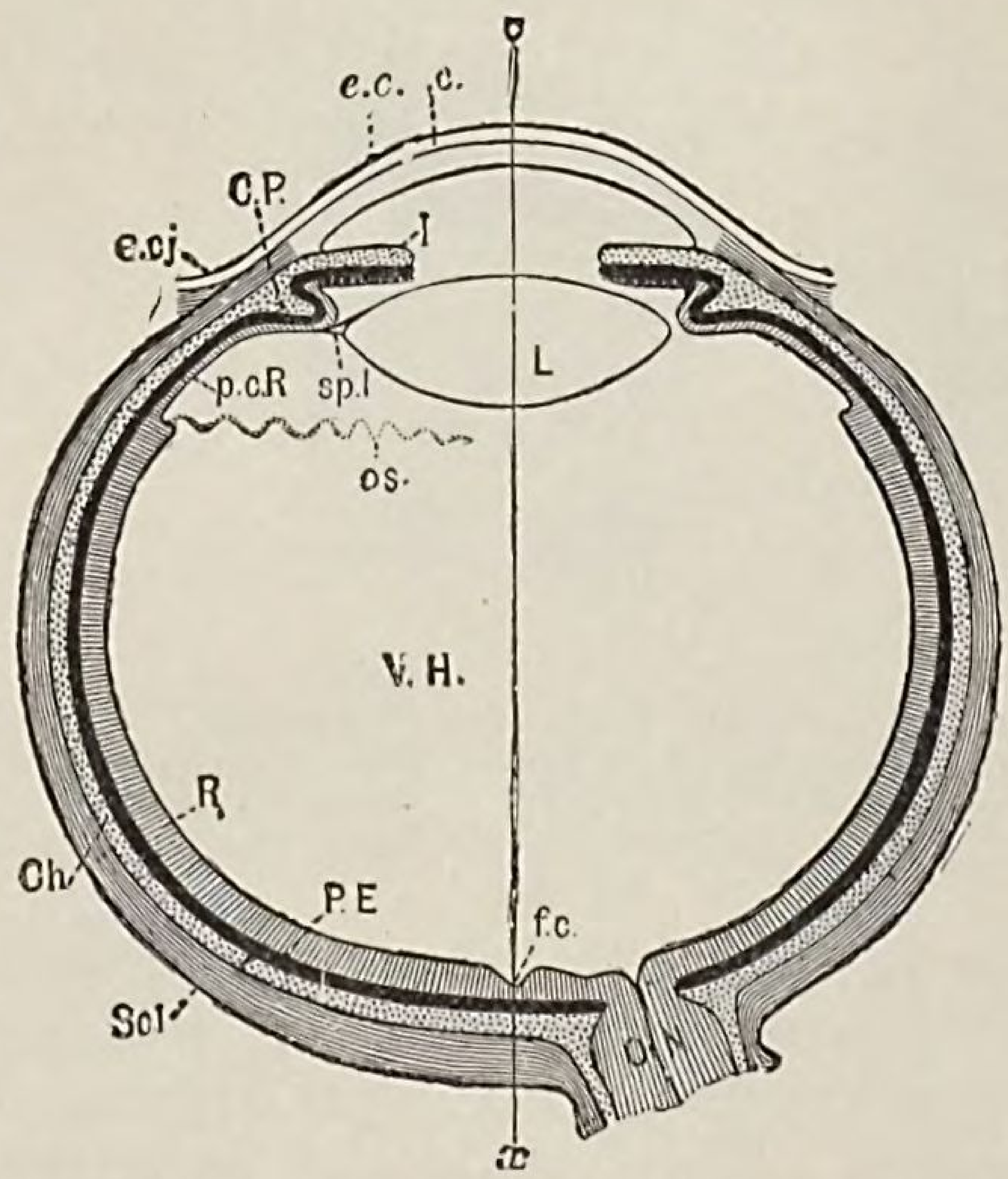


FIG. 739.—Diagrammatic horizontal section of the eye of **Man**. *c.* cornea; *ch.* choroid (dotted); *C.P.* ciliary processes; *e. c.* epithelium of cornea; *e. cj.* conjunctiva; *f. o.* yellow spot; *I.* iris; *L,* lens; *ON.* optic nerve; *OS.* ora serrata; *o—x,* optic axis; *p. c. R,* anterior non-visual portion of retina; *P.E.* pigmented epithelium (black); *R.* retina; *sp. l.* suspensory ligament; *Scl.* sclerotic; *V. H,* vitreous. (From Foster and Shore's *Physiology*.)

Lining the choroid and forming the innermost coat of the eye is a delicate semi-transparent membrane, the *retina* (*R.*) covered on its outer or choroidal surface with a layer of black pigment (*P. E.*). It extends as far as the outer ends of the ciliary processes where it appears to end in a wavy line, the *ora serrata* (*O. S.*): actually, however, it is continued as a very delicate membrane (*p. c. R*) over the ciliary processes and the posterior face of the iris. The optic nerve (*ON.*) pierces the sclerotic and choroid and becomes continuous with the retina, its fibres spreading over the inner surface of the latter. Microscopic examination shows that these fibres, which form the innermost layer of the retina (Fig. 740, *o. n.*), turn outwards and become connected with a layer of nerve-cells (*n. c.*). External to these come other layers of nerve-cells and granules, supported by a framework of delicate fibres, and finally, forming the outer surface of the retina proper, a layer of bodies called, from their shape, the *rods* and *cones* (*r.*). These are placed perpendicularly to the surface of the retina, and their outer ends are imbedded in a single layer of hexagonal *pigment cells,* loaded with granules of the black pigment already referred to.

Immediately behind and in close contact with the iris is the transparent biconvex *lens* (Fig. 739, *L.*), formed of concentric layers of fibres each derived from a single cell. The lens is enclosed in a delicate *capsule*, attached by a *suspensory ligament* (*sp. l.*) to the ciliary processes. The suspensory ligament exerts a pull upon the elastic lens so as to render it less convex than when left to itself; when the ciliary muscles contract they draw the suspensory ligament towards the iris and allow the lens to assume its normal

curvature. It is in this way that the accommodation of the eye to near and distant objects is effected.

The space between the cornea in front and the iris and lens behind is called the *anterior chamber* of the eye, and is filled by a watery fluid—the *aqueous humour*. The main cavity of the eye, bounded in front by the lens and the ciliary processes and for the rest of its extent by the retina, is called the *posterior chamber*, and is filled by a gelatinous substance, the *vitreous humour* (*V. H.*).

The cornea, aqueous, lens, and vitreous together constitute the dioptric apparatus of the eye, and serve to focus the rays of light

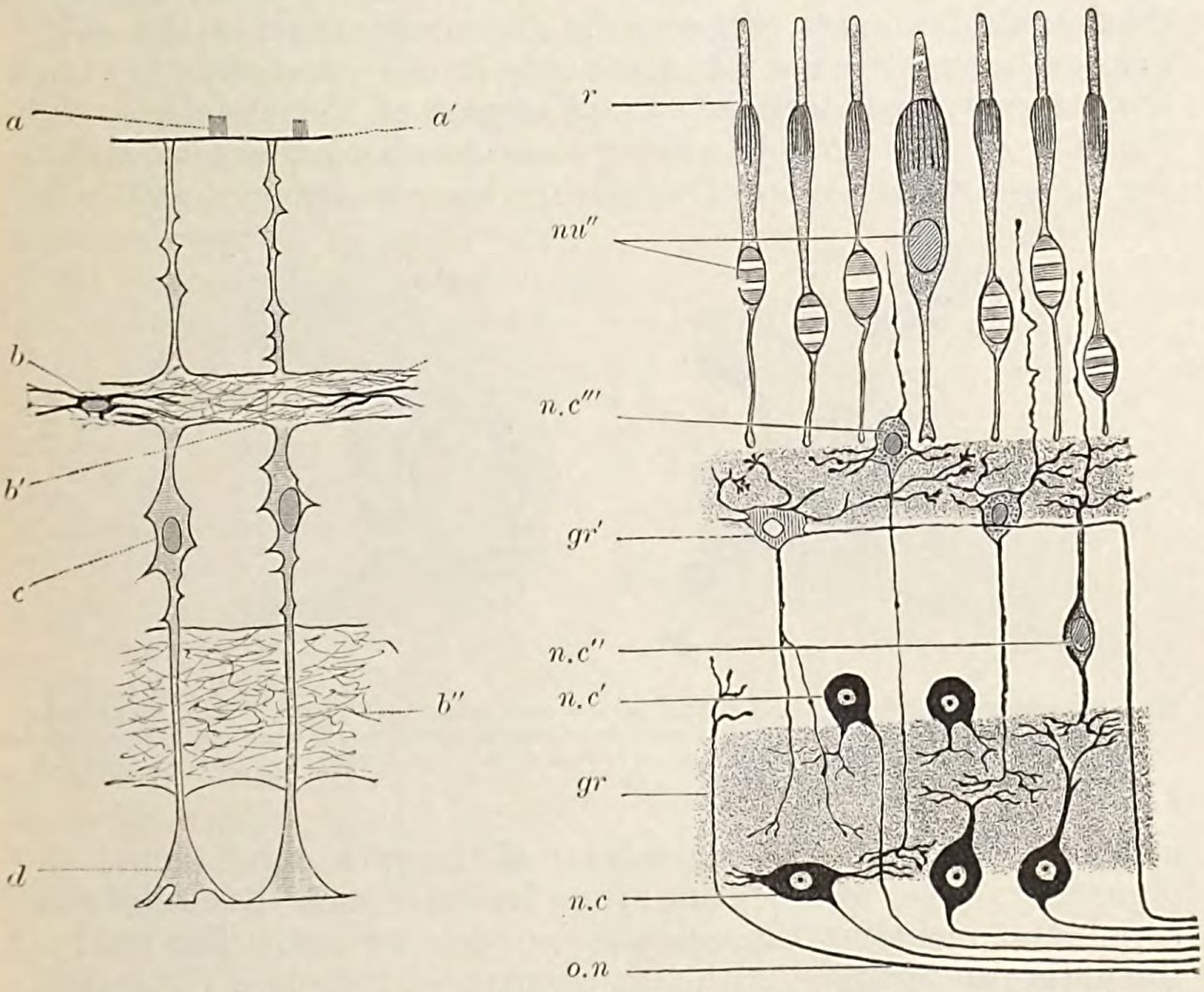


FIG. 740.—Diagram of the retina, the supporting structures to the left, the nervous and epithelial elements to the right; *a—d.* fibrous supporting structures; *gr. gr'.* granular layers; *n.c. n.c'. n.c''. n.c'''.* nerve cells; *nu.* nuclear layer of rods and cones; *o.n.* fibres of optic nerve; *r.* rods and cones. (From Wiedersheim's *Vertebrata.*)

from external objects on the retina. The iris is the diaphragm by which the amount of light entering the eye is regulated. The percipient portion or actual organ of sight is the retina, or, more strictly, the layer of rods and cones. The great peculiarity of the vertebrate eye, as compared with that of a Cephalopod (Vol. I, p. 720), to which it bears a close superficial resemblance, is that the sensory cells form the outer instead of the inner layer of the retina, so that the rays of light have to penetrate the remaining layers before affecting them.

The mode of development of the eye is as characteristic as its structure. At an early stage of development a hollow outgrowth—the *optic vesicle* (Fig. 741, A, *opt. v*)—is given off from each side of the diencephalon (*dien.*). It extends towards the side of the head, where it meets with an in-pushing of the ectoderm (*inv. l.*) which deepens and forms a pouch, and finally, separating from the ectoderm, a closed sac (B, *l.*) with a very small cavity and thick walls. This sac is the rudiment of the lens: as it enlarges it pushes against the optic vesicle, and causes it to become invaginated (*B*), the single-layered optic vesicle thus becomes converted into a two-layered *optic cup* (*opt. c.*, *opt. c*[1].), its cavity, originally continuous with the diacœle, becoming obliterated. The invagination of the vesicle to form the cup does not take place symmetically, but obliquely from the external (posterior) and ventral aspect of the vesicle, so that the optic cup is incomplete along one side where there is a cleft—the *choroid fissure*—afterwards more or less completely closed by the

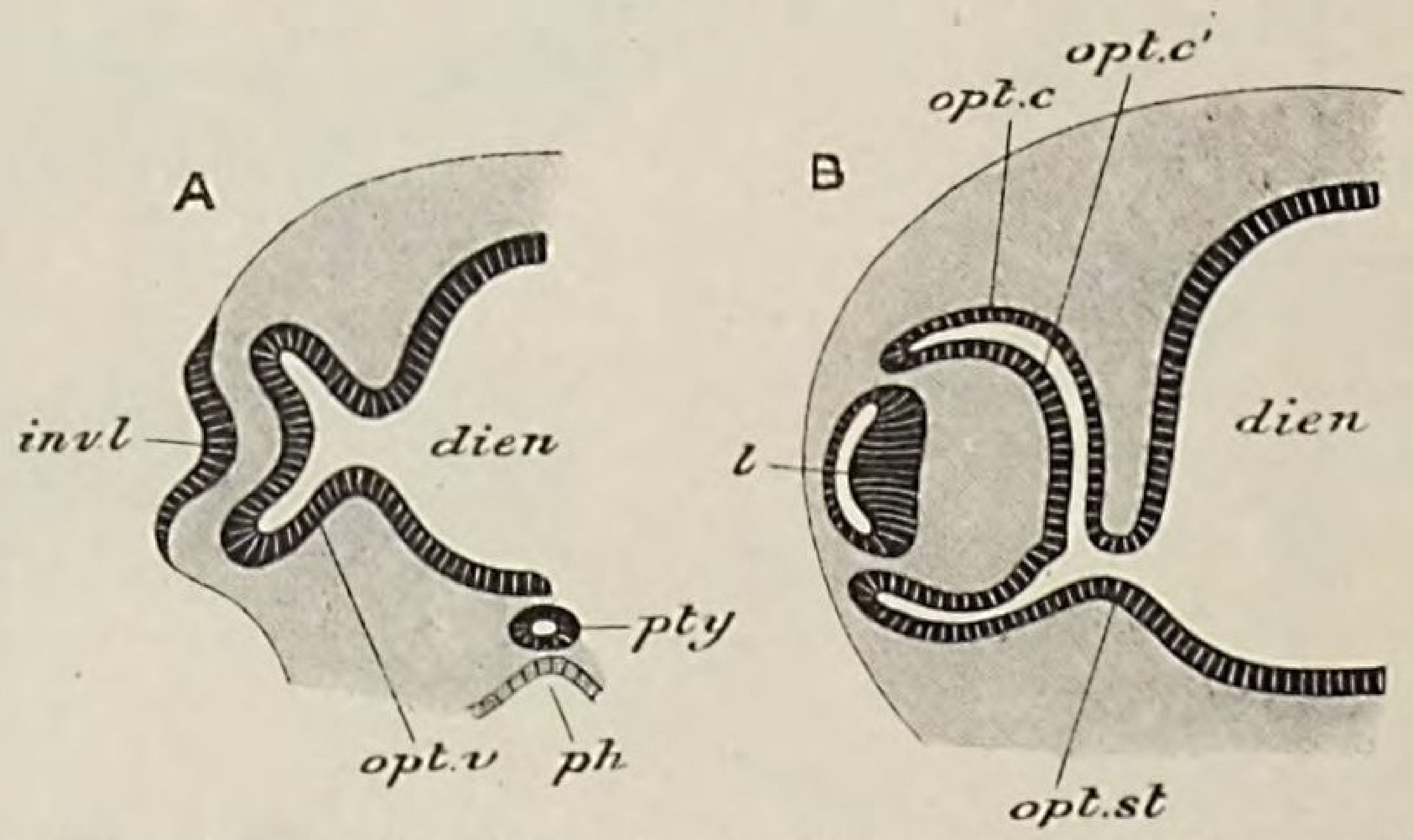


FIG. 741.—Early (A) and later (B) stages in the development of the eye of a **Craniate**. *dien.* diencephalon; *inv. l.* invagination of ectoderm to form lens; *l.* lens; *opt. c.* outer layer of optic cup; *opt. c'.* inner layer; *opt. st.* optic stalk; *opt. v.* optic vesicle; *ph.* pharynx; *pty.* pituitary body. (Altered from Marshall.)

union of its edges. The outer layer of the optic cup becomes the pigmentary layer of the retina: from its inner layer the rest of that membrane, including the rods and cones, is formed. The stalk of the optic cup occupies, in the embryonic eye, the place of the optic nerve, but the actual fibres of the nerve are formed as backward growths from the nerve-cells of the retina to the brain.

During the formation of the lens, mesoderm grows in between the pouch from which it arises and the external ectoderm; from this the main substance of the cornea and its inner or posterior epithelium are formed, the adjacent ectoderm becoming the external epithelium. Mesoderm also makes its way into the optic cup, through the choroid fissure, and becomes the vitreous. Lastly, the mesoderm immediately surrounding the optic cup is differentiated to form the choroid, the iris, and the sclerotic.

Thus the paired eye of Vertebrates has a threefold origin: the sclerotic, choroid, iris, vitreous, and the greater part of the cornea

are mesodermal: the lens and external epithelium of the cornea are derived from the ectoderm of the head: the retina and optic nerve are developed from a hollow pouch of the brain, and are therefore, in their ultimate origin, ectodermal. The sensory cells of the retina, the rods and cones, although not directly formed from the external ectoderm, as in Invertebrates, are ultimately traceable into the superficial layer of ectoderm, since they are developed from the inner layer of the optic vesicle, which is a prolongation of the inner layer of the brain, which is continuous, before the closure of the medullary groove, with the ectoderm covering the general surface of the body.

The eye-ball is moved by six muscles (Fig. 742). Four of these arise from the inner wall of the orbit, and pass, diverging as they go, to their insertion round the equator of the eye. One of them is dorsal in position, and is called the *superior rectus* (*s. r.*) a second ventral, the *inferior rectus* (*in. r.*), a third anterior, the *anterior* or *internal rectus* (*i. r.*), and a fourth posterior, the *posterior* or *external rectus* (*e. r*). The usual names (internal and external) of the two last-named muscles originate from their position in Man, where, owing to the eye looking forwards instead of outwards, its anterior surface becomes internal, its posterior surface external. The two remaining muscles usually arise from the anterior (in Man inner) corner of the orbit, and are inserted respectively into the dorsal and ventral surface of the eye-ball. They are the *superior* (*s. o.*) and *inferior oblique* (*i. o.*) muscles.

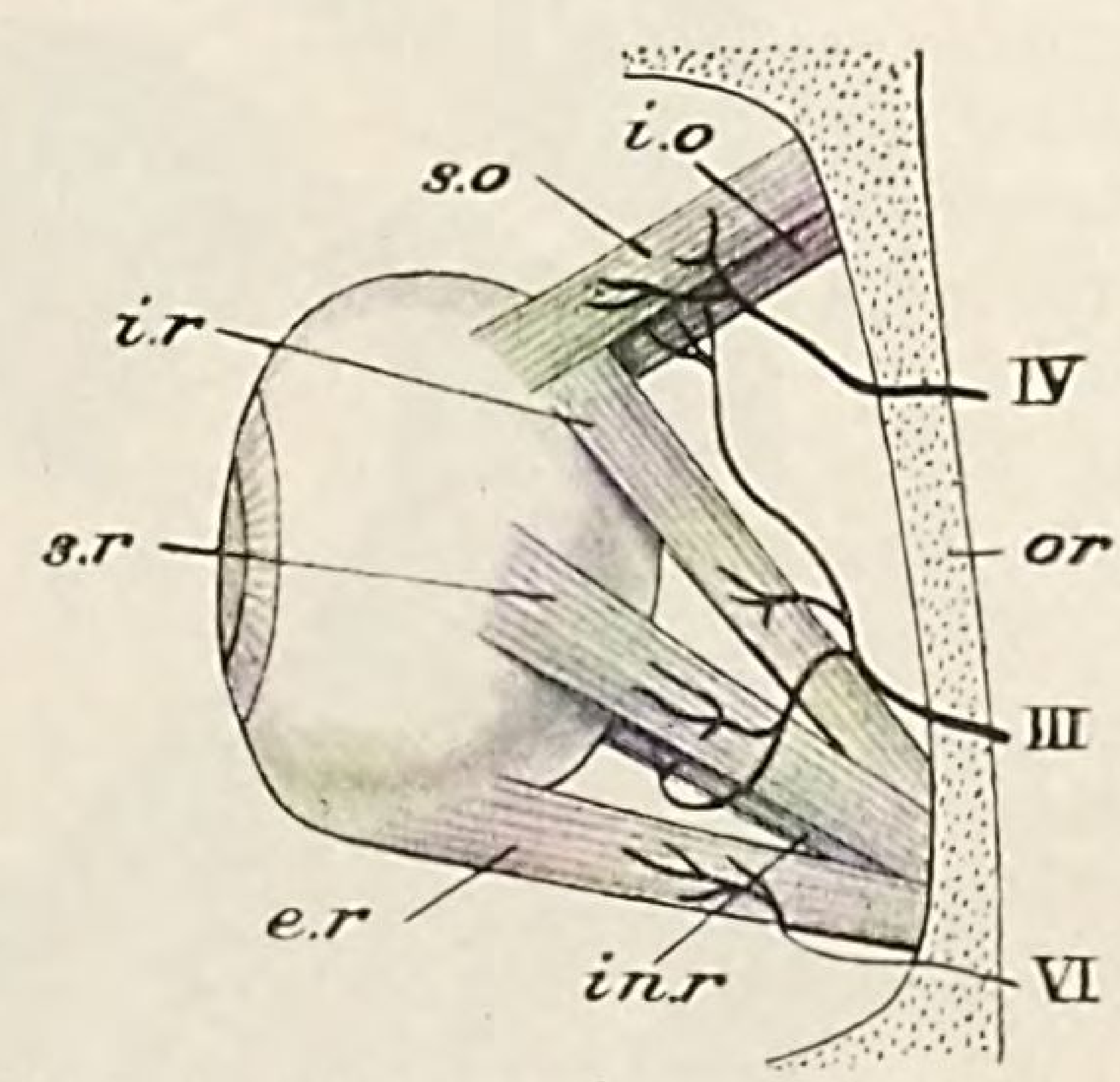


FIG. 742.—Muscles of the eye of a **Skate** and their nerves (semi-diagrammatic). *III*, oculomotor nerve; *IV*, trochlear; *VI*, abducent. *e. r.* external rectus; *in. o.* inferior oblique; *in. r.* inferior rectus; *i. r.* internal rectus; *or.* wall of orbit; *s. o.* superior oblique; *s. r.* superior rectus.

The *median* or *pineal eye* (Fig. 743), is formed, in certain cases, from the distal end of the epiphysial diverticulum already mentioned. It has the form of a rounded capsule, the outer or anterior portion of the wall of which is a lens (*l.*) formed of elongated cells, while its posterior portion has the character of a retina (M, *r*). The latter has a layer of nerve fibres on its outer, and one of rod-like visual elements (*r.*) on its inner surface: it thus agrees with the usual types of Invertebrate retina, and not with that of the paired eye.

The **organ of hearing**, like that of sight, presents quite peculiar features. It arises in the embryo as a paired invagination of the

ectoderm in the region of the hind-brain, a shallow depression being formed which deepens and becomes flask-shaped, and finally, as a rule, loses its connection with the external ectoderm, becoming a closed sac surrounded by mesoderm. At first simple, it soon becomes divided by a constriction into dorsal and ventral compartments. The dorsal compartment is differentiated into an irregular chamber, the *utriculus* (Fig. 744, *u.*), and, usually, three tubes, the *semicircular canals.* Of these two, the *anterior* (*ca.*)

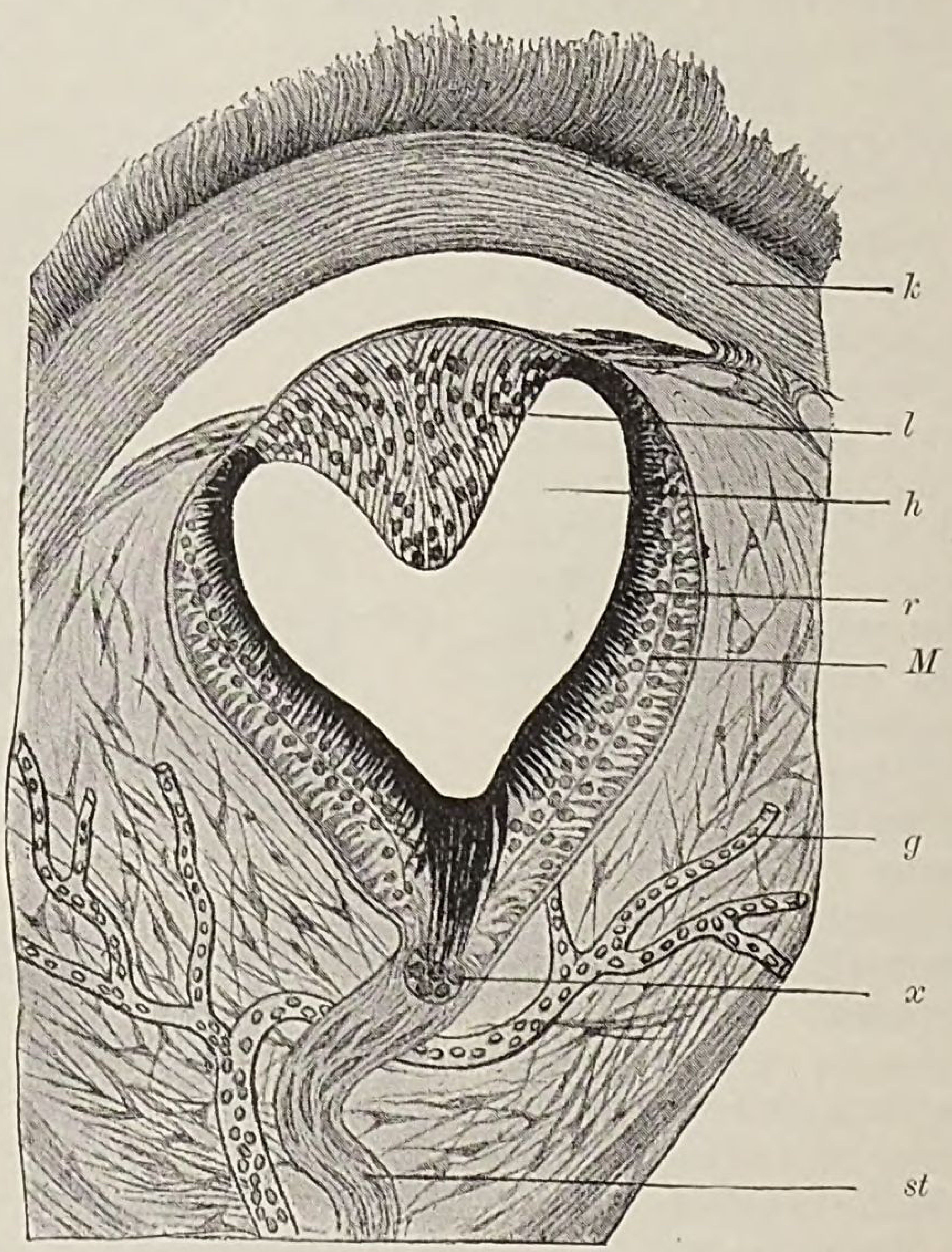


FIG. 743.—Section of the pineal eye of **Hatteria**. *g*, blood-vessel; *h*, cavity of eye, filled with fluid; *k*, connective tissue capsule; *l*. lens; *M*. molecular layer of retina; *r*, layer of rods and cones; *st*, nerve; *x*, cells in nerve. (From Wiedersheim's *Vertebrata*, after Baldwin Spencer.)

and *posterior* (*ap.*) *canals*, are vertical in position and have their adjacent limbs united so that the two canals have only three openings between them into the utriculus: the third or *external canal* (*ae.*) is horizontal, and opens into the utriculus at either end. Each canal is dilated at one of its ends into an *ampulla* (*ae.*, *ac.*, *ap.*), placed anteriorly in the anterior and external canals, posteriorly in the posterior canal.

The ventral compartment of the auditory sac is called the *sacculus* (*s.*): it gives off posteriorly a blind pouch, the *cochlea* (*l.*),

which attains considerable dimensions in the higher classes, while from its inner face is given off a narrow tube, the *endolymphatic duct* (*de.*), which either ends blindly or opens on the dorsal surface of the head. The utricle and sacculi are sometimes imperfectly differentiated, and are then spoken of together as the *vestibule.*

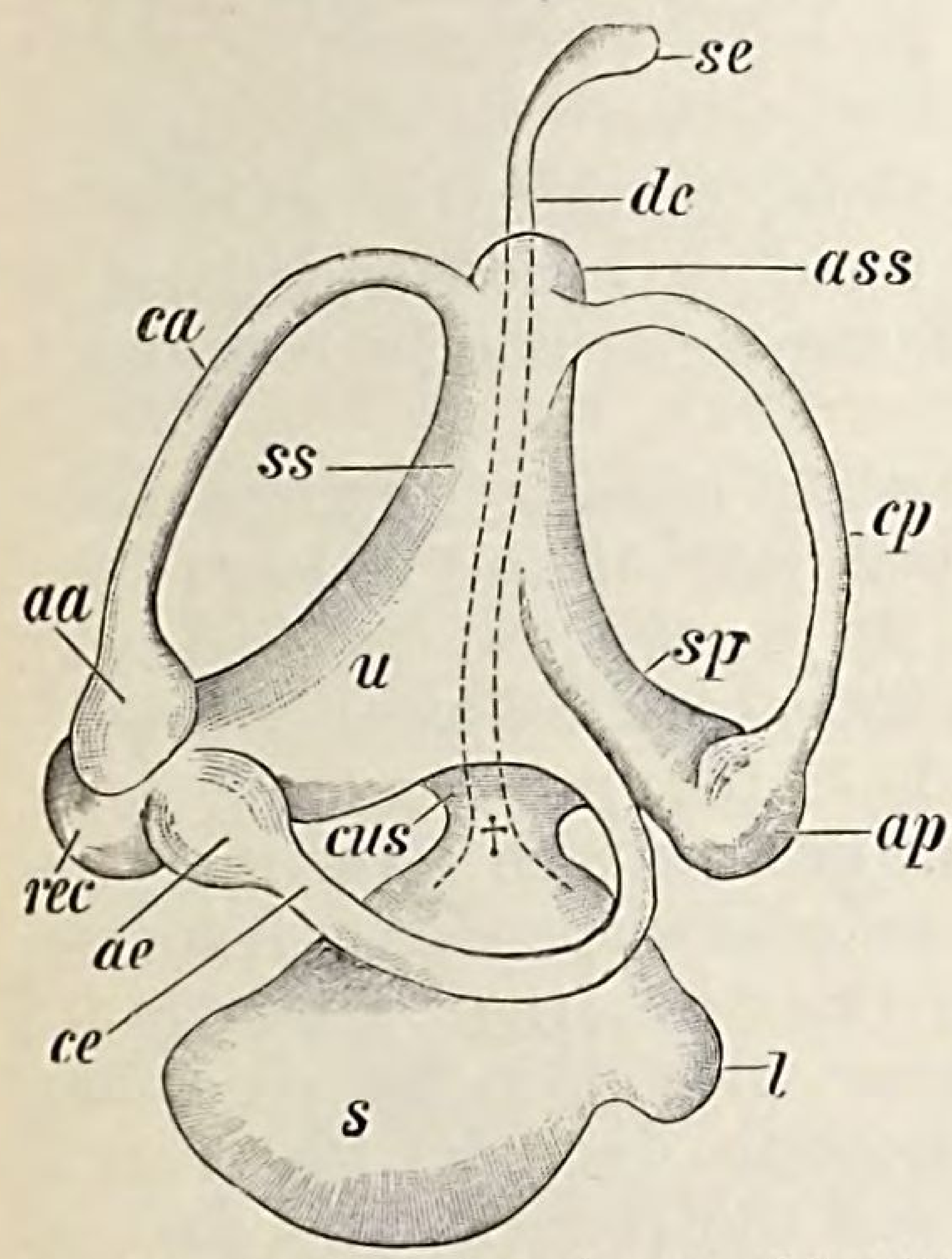


FIG. 744.—External view of organ of hearing of **Craniata** (semi-diagrammatic). *aa*, ampulla of anterior canal; *ae*, of horizontal canal; *ap*, of posterior canal; *ass.* apex of superior utricular sinus; *ca*, anterior semicircular canal; *ae*, horizontal; *ap*, posterior; *cus*, canal uniting sacculus with utriculus; *de*, endolymphatic duct; *l*, cochlea; *rec.* utricular recess; *s*, sacculus; *se*, endolymphatic sac; *sp*, posterior utricular sinus; *ss.* superior utricular sinus; *u.* utriculus. (From Wiedersheim's *Vertebrata.*)

Patches of sensory cells (Fig. 745, *ae.*)—elongated cells produced into hair-like processes (*a. h.*)—occur in the ampulla and in the utricle and saccule: they are known as *maculæ acusticæ* and *cristæ acusticæ* (*c. r.*), and to them the fibres of the auditory nerve (*n.*) are distributed. A fluid, the *endolymph,* fills the whole of the auditory organ, or *membranous labyrinth,* and in it are formed otoliths of varying size and number. There is every reason for thinking that the labyrinth, as in the lower animals, functions as an organ of equilibration as well as of hearing.

As the membranous labyrinth develops in the embryo it becomes surrounded and enclosed by the auditory capsule, the cartilage of which adapts itself to the form of the labyrinth, presenting a large excavation for the utricle and saccule and tunnel-like passages for the canals. The auditory organ does not, however, fit tightly into this system of cavities, but be-

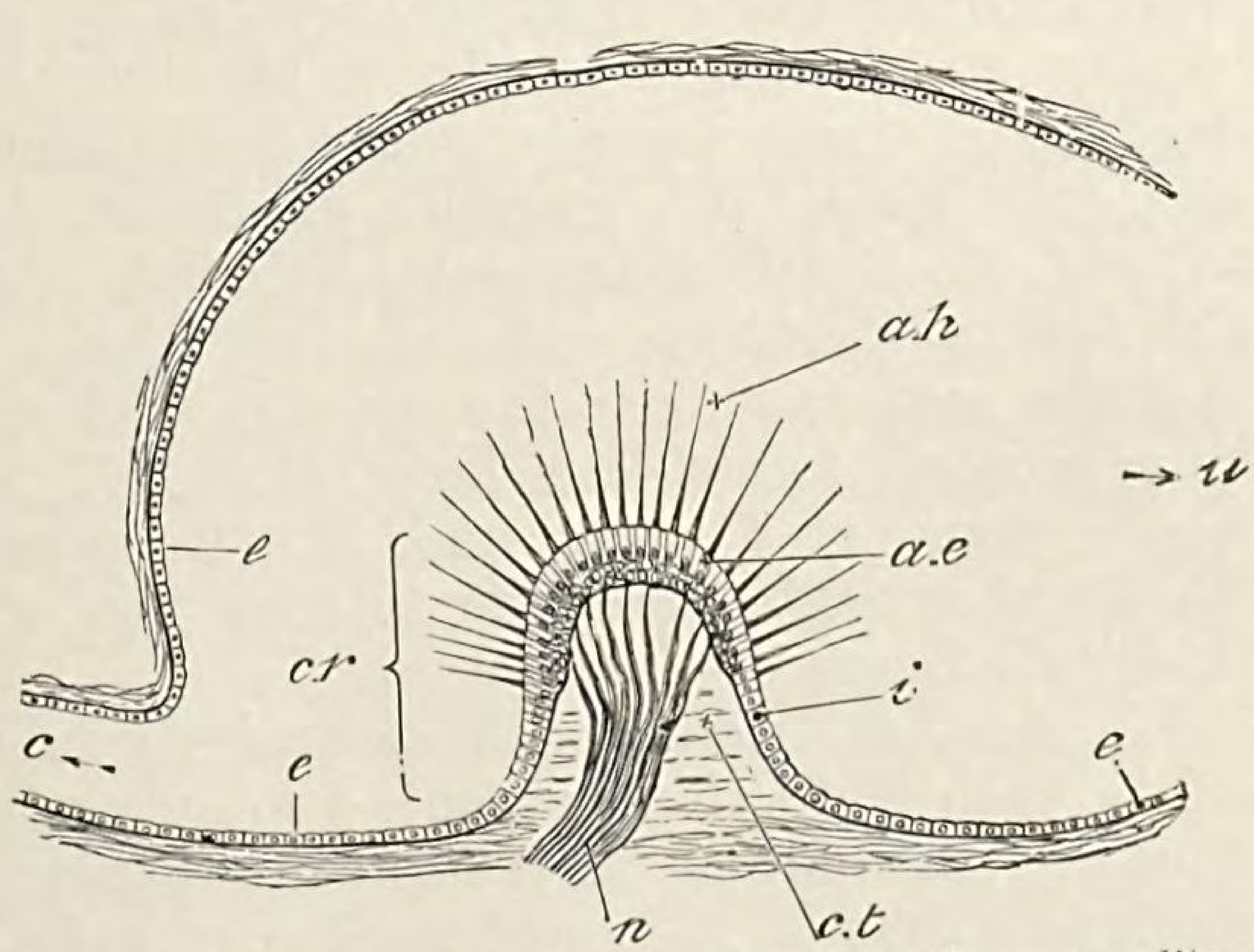


FIG. 745.—Longitudinal section through an ampulla. *a. e.* auditory epithelium; *a. h.* auditory hairs; *c.* part of semicircular canal; *cr.* crista acustica; *ct.* connective tissue; *e. i,* epithelium; *n.* nerve; *u.* junction with utriculus. (From Foster and Shore's *Physiology.*)

tween it and the cartilage is a space, filled by a fluid called *perilymph*, which acts as a buffer to the delicate organ floating in it.

Urinogenital Organs.—In all Craniata there is so close a connection between the organs of renal excretion and those of reproduction that the two systems are conveniently considered together as the urinogenital organs.

Speaking generally, the excretory organ consists of three parts, all paired and situated along the dorsal wall of the cœlome; the *fore-kidney* or *pronephros* (Fig. 715, A, *p. nph.*), the *mid-kidney* or *mesonephros* (*ms. nph.*), and the *hind-kidney* or *metanephros* (*mt. nph.*). Each of these is provided with a duct, the *pro-* (*pn. d.*), *meso-* (*msn. d.*), and *meta-nephric* (*mt. n. d.*) *ducts*, which open into the cloaca. The gonads (*gon.*) lie in the cœlome suspended to its dorsal wall by a fold of peritoneum: in some cases their products are discharged into the cœlome and make their exit by abdominal pores, but more usually the pronephric duct in the female assumes the functions of an oviduct and the mesonephric duct in the male those of a spermiduct. The pronephros is almost always functionless in the adult, and usually disappears altogether. The mesonephros is usually the functional kidney in the lower Craniata, in which, as a rule, no metanephros is developed, and the mesonephric duct, in addition to carrying the seminal fluid of the male, acts as a ureter. In the higher forms the mesonephros atrophies, and the metanephros is the functional kidney, the metanephric duct becoming the ureter.

The *kidney*—meso- or meta-nephros—of the adult is a massive gland of a deep red colour made up of convoluted *urinary tubules* (Fig. 746), separated from one another by connective tissue containing an abundant supply of blood vessels. The tubules are lined by a single layer of glandular epithelial cells (B, C) and each ends blindly in a globular dilatation, the *Malpighian capsule* (A, *gl.*), lined with squamous epithelium. In many of the lower Craniata, a branch goes off from the tubule, near the Malpighian capsules, and, passing to the ventral surface of the kidney, ends in a ciliated funnel-like body (Fig. 747, *nst.*), resembling the nephrostome of a worm, and, like it, opening into the cœlome. At their opposite ends the tubules join with one another, and finally discharge into the ureter.

The renal arteries branch extensively in the kidney, and give off to each Malpighian capsule a minute *afferent artery* (Fig. 746, A, *v. a.*): this pushes the wall of the capsule before it, and breaks up into a bunch of looped capillaries, called the *glomerulus*, suspended in the interior of the capsule. The blood is carried off from the glomerulus by an *efferent vessel* (*v. e.*), which joins the general capillary system of the kidneys, forming a network over the

urinary tubules: finally, the blood is returned from this network to the renal vein. The watery constituents of the urine are separated from the blood in traversing the glomerulus, and, flowing down the tubule, take up and dissolve the remaining constituents—urea, uric acid, &c.—which are secreted by the cells of the tubules.

The development of the kidney reveals a resemblance to the nephridia of worms which would hardly be suspected from its adult structure. The pronephros (Fig. 747, A, *p. nph.*) originates as two or three coiled tubes formed from mesoderm in the body-wall at the anterior end of the cœlome; they are arranged metamerically and each opens into the cœlome by a ciliated funnel

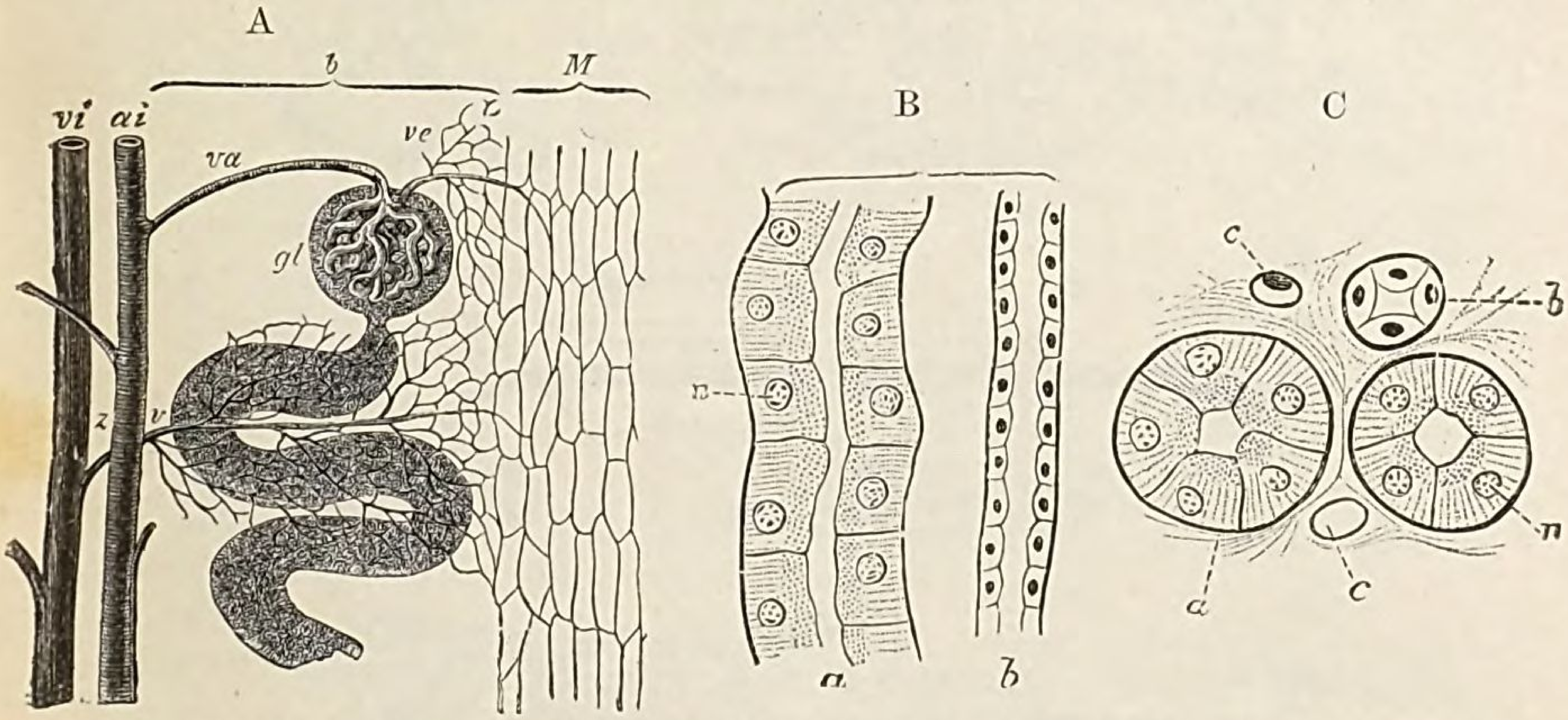


FIG. 746.—A, part of a urinary tubule with blood-vessels. *ai*, artery; *gl*, Malpighian capsule containing glomerulus; *v*. veinlet returning blood from capillary network (to the right) to vein *vi*; *va*, afferent vessel of glomerulus; *ve*, efferent vessel. B, longitudinal, and C, transverse sections of urinary tubules. *a*, secreting part of tubules; *b*, conducting part of tubules; *c*. capillaries; *n*. nuclei. (From Foster and Shore's *Physiology*.)

(*nst.*). Obviously such tubes are *mesonephridia*: their chief peculiarity is that their outer ends do not open directly on the exterior, but into a longitudinal tube, the *archinephric* or *segmental duct* (*sg. d.*), which passes backwards and discharges into the cloaca. It seems probable that this arrangement is to be explained by supposing that the nephridia originally opened externally into a longitudinal groove, which, by the apposition of its edges, was converted into a tube. All three nephridia of the pronephros open, by their ciliated funnels, into the narrow anterior end of the cœlome, into which projects a branch of the aorta ending in a single large glomerulus.

The pronephros soon degenerates, its nephridia losing their connection with the segmental duct (B), but in the meantime fresh nephridia appear in the segments posterior to the pronephros, and together constitute the mesonephros or *Wolffian body*

(B, *ms. nph.*) from which the permanent kidney is formed in most of the lower Craniata. The mesonephric nephridia open at one

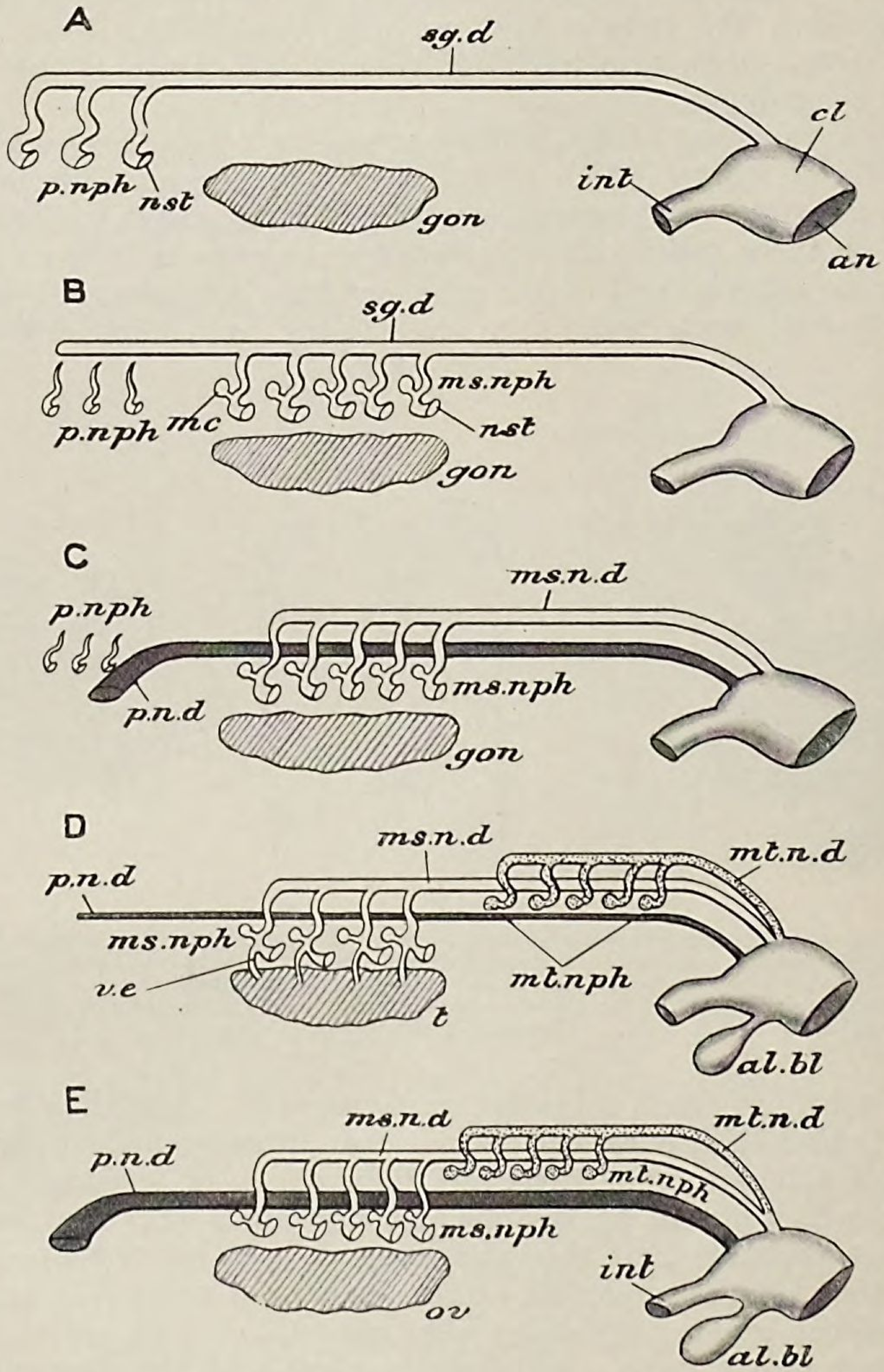


FIG. 747.—Diagrams illustrating the development of the urinogenital organs of **Craniata**. A, development of pronephros and segmental duct; B, atrophy of pronephros, development of mesonephros; C, differentiation of pro- and meso-nephric ducts; D, development of metanephros, male type; E, female type. *al. bl.* allantoric bladder; *an.* anus; *cl.* cloaca; *gon.* gonad; *int.* intestine; *m. c.* Malpighian capsule; *ms. n. d.* mesonephric duct; *ms. nph.* mesonephros; *mt. n. d.* metanephric duct; *mt. nph.* metanephros; *nst.* nephrostome; *ov* ovary; *p. n. d.* pronephric duct; *p. nph.* pronephros; *sg. d.* segmental duct; *t.* testis; *v. e.* vasa efferentia.

end into the segmental duct (*sg. d.*), at the other, by ciliated funnels (*nst.*), into the cœlome; a short distance from the funnel

each gives off a blind pouch which dilates at the end and forms a Malpighian capsule (*m. c.*), and a branch from the aorta entering it gives rise to a glomerulus.

In some forms the archinephric duct now becomes divided by a longitudinal partition into two tubes: one retains its connection with the mesonephros and is known as the mesonephric or *Wolffian duct* (C, *ms.n.d.*): the other has no connection with the nephridia, but opens into the cœlome in the region of the vanishing pronephros: it is the pronephric or *Müllerian duct* (*p. n. d.*). In some Craniata the Müllerian appears quite independently of the Wolffian duct: the latter is then simply the segmental duct after the union with it of the mesonephric tubules.

In the higher Vertebrata, from Reptiles to Mammals, a diverticulum (D, E, *mt. n. d.*) is given off from the posterior end of the Wolffian duct, which grows forwards and becomes connected with the hindmost nephridia. In this way is formed a metanephros (*mt. nph.*), which becomes the permanent kidney, and a metanephric duct (*mt. n. d.*), which becomes the ureter. The Wolffian body ceases to discharge a renal function, and becomes a purely vestigial organ.

In many Fishes there is a dilatation of the ureter, the *urinary bladder*, which serves as a receptacle for the urine. In the higher Craniata the ventral wall of the cloaca sends off a pouch, the *allantoic bladder* (*al. bl.*), which serves the same purpose although morphologically an entirely different structure.

The *gonads* (*gon.*) are developed as ridges growing from the dorsal wall of the cœlome, and covered by cœlomic epithelium, from the cells of which, as in so many of the lower animals, the ova and sperms are derived. The testis consists of crypts or tubules, lined with epithelium, and usually discharging their products, through delicate *vasa efferentia* (D, *v. e.*), into the Wolffian duct, but in some groups into the cœlome. The sperms are always motile. The ovary is formed of a basis of connective tissue or *stroma*, covered by epithelium, certain of the cells of which become enlarged to form ova. In the majority of cases the ova are discharged from the surface of the ovary into the open ends of the Müllerian ducts (E, *p. n. d.*), which thus function simply as oviducts, having no connection in the adult with the urinary system. In some groups the ova, like the sperms, are shed into the cœlome and escape by the genital pores, and in many teleostean or bony Fishes, the ovary is a hollow organ, as in Arthropoda, discharging its ova into an internal cavity, whence they are carried off by a duct continuous with the gonad.

A few Craniata are normally hermaphrodite, but the vast majority are diœcious, hermaphroditism occurring, however, occasionally, as an abnormality.

In close connection with the urinogenital organs are found

certain "ductless glands," the *adrenals* or *supra-renal bodies.* They are developed partly from ridges of the dorsal wall of the cœlome—*i.e.*, from mesoderm, partly from the sympathetic ganglia. There may be numerous adrenals segmentally arranged, or a single pair. Their function is quite unknown, but their abundant blood-supply points to their possessing a high physiological importance.

Development.—The ova of Craniata are usually telolecithal, but the amount of food-yolk varies within wide limits. When it is small in quantity segmentation is complete but usually unequal, when abundant, incomplete and discoidal. In the latter case the embryo proper is formed, as in Cephalopods, from a comparatively small portion of the oosperm, the rest giving rise to a large yolk-sac.

There is never a typical invaginate gastrula, as in Amphioxus, but in some of the lower Craniata a gastrula stage is formed by a

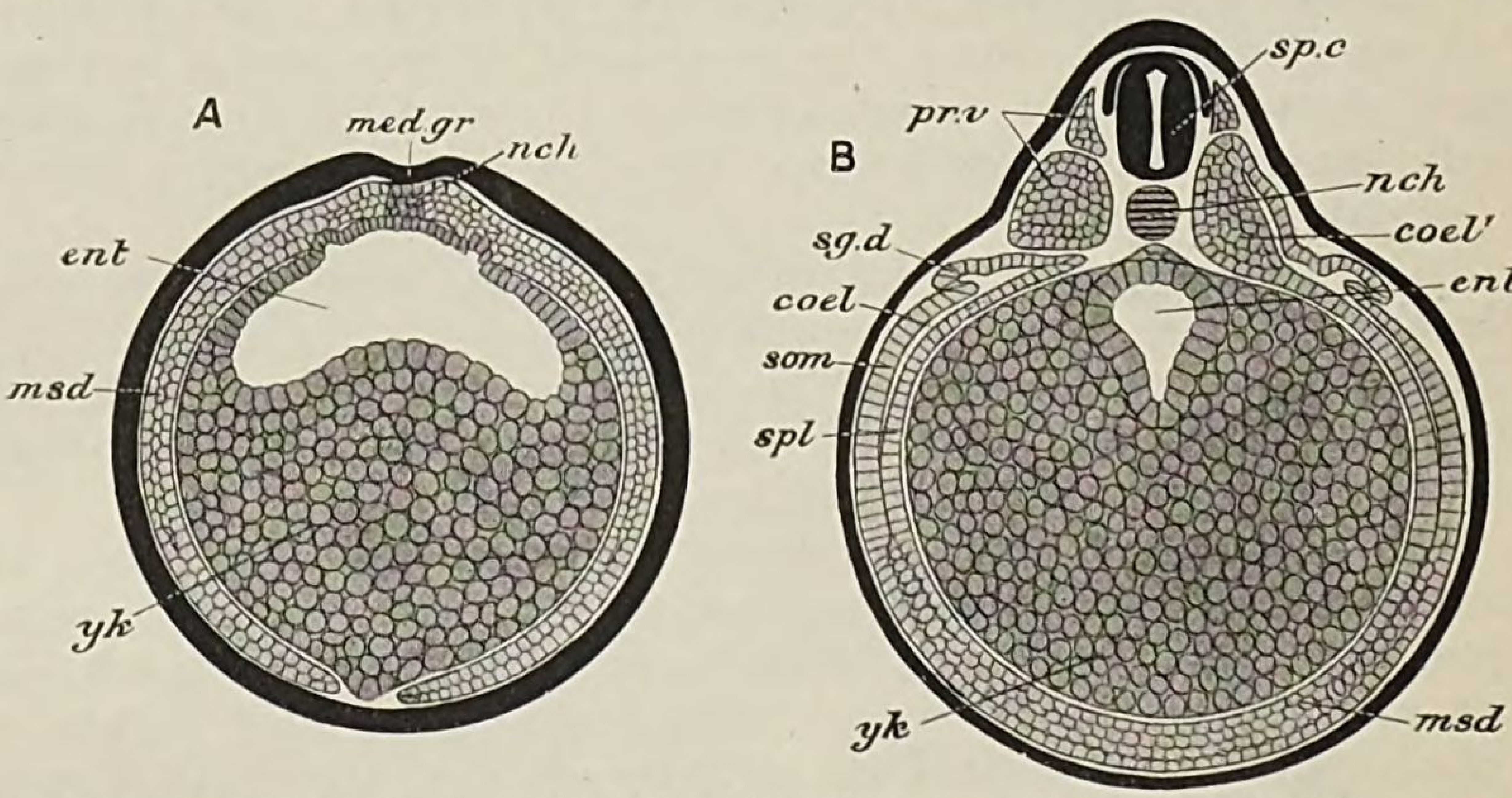


FIG. 748.—Transverse section of earlier (A) and later (B) embryos of **Frog**. *cœl.* cœlome ; *cœl'.* prolongation of cœlome into protovertebra ; *ent.* mesenteron ; *med. gr.* medullary groove ; *msd.* mesoderm ; *nch.* notochord ; *pro.* protovertebra ; *sg. d.* segmental duct ; *som.* somatic layer of mesoderm ; *sp. c.* spinal cord ; *spl.* splanchnic layer of mesoderm ; *yk.* yolk cells. (After Marshall.)

combination of in-pushing and over-growth: the details will be given in the sections on the various groups. In the higher forms a gastrula cannot be recognised with absolute certainty.

The mode of development of the mesoderm and of the cœlome differs strikingly from the process we are familiar with in Amphioxus. At an early stage the mesoderm is found in the form of paired longitudinal bands (Fig. 748, A, *msd.*) lying one on each side of the middle line, where they are separated from one another by the medullary tube (*md. gr.*) and the notochord (*nch.*), and completely filling the space between the ectoderm and the endoderm. In all probability the mesoderm is derived from both of the primitive germ-layers. Each mesoderm band becomes differentiated into a dorsal portion, the *vertebral plate,* bounding the nervous

system and notochord, and a ventral portion, the *lateral plate*, bounding the mesenteron. The vertebral plate undergoes metameric segmentation, becoming divided into a row of squarish masses, the *protovertebræ* or *mesodermal segments* (B, *pr. v.*): the lateral plate splits into two layers, a somatic (*som.*) adherent to the ectoderm, a splanchnic (*spl.*) to the endoderm. The space between the two is the cœlome (*cœl.*), which is thus a *schizocœle* or cavity hollowed out of the mesoderm and is at no stage in communication with the mesenteron, like the cœlomic pouches of Amphioxus. A dorsal offshoot of the cœlome (*cœl′*) may pass into each protovertebra, but such an arrangement is temporary. From the dorsal portions of the protovertebræ the myomeres are formed, from their ventral portions the vertebræ.

The development of the principal organs has been described, in general terms, in the preceding account of the organs themselves: it will be convenient to defer further consideration of this subject until we come to deal with the development of the various types of Craniata, and with the embryological characteristics of the classes and sub-classes.

Distinctive characters.—The Craniata may be defined as Vertebrata in which the notochord is not continued to the end of the snout, but stops short beneath the fore-brain, some distance from its anterior end. A skull is always present, and there are usually paired limbs. The ectoderm is many-layered and is never ciliated in the adult, and only rarely in the larva. The pharynx is of moderate dimensions, and is perforated by not more than seven pairs of gill-slits. There is no atrium. The liver is large, massive, and not obviously tubular. There is a muscular chambered heart, and the blood contains red corpuscles. The nephridia (mesonephridia) unite to form large paired kidneys and open into ducts which discharge into or near the posterior end of the intestine. The brain is complex, and there are at least ten pairs of cerebral nerves: the spinal nerves are, except in Cyclostomes, formed by the union of dorsal and ventral roots. Paired eyes of great complexity, derived in part from the brain, are present, and there is a pair of auditory organs. There is a single pair of gonads, and the reproductive products are usually discharged by ducts derived from the nephridial system. There is never a typical invaginate gastrula, and the mesoderm arises in the form of paired longitudinal bands which subsequently become segmented. The cœlome is a schizocœle.

CLASS I.—CYCLOSTOMATA.

The Cyclostomata, or Lampreys and Hags, are eel-like Fishes, distinguished from all other Craniata by the possession of a suctorial mouth devoid of functional jaws, by the single olfactory organ, and by the absence of lateral appendages or paired fins.

1. EXAMPLE OF THE CLASS.—THE LAMPREY (*Petromyzon*).

Three species of Lamprey are common in the Northern Hemisphere: the Sea-lamprey (*P. marinus*), which attains a length of a metre; the Lampern, or common fresh-water Lamprey (*P. fluviatilis*), about 60 cm. in length; and the Sand-pride, or lesser fresh-water Lamprey (*P. branchialis*), not exceeding 30 cm. in length. In the Southern Hemisphere the Lampreys belong to two genera: *Mordacia*, found on the coasts of Chili and Tasmania, and *Geotria*, in the rivers of Chili, Australia, and New Zealand. Both genera differ from Petromyzon in minor details only.

External characters.—The head and trunk (Fig. 749) are nearly cylindrical, the tail-region compressed or flattened from

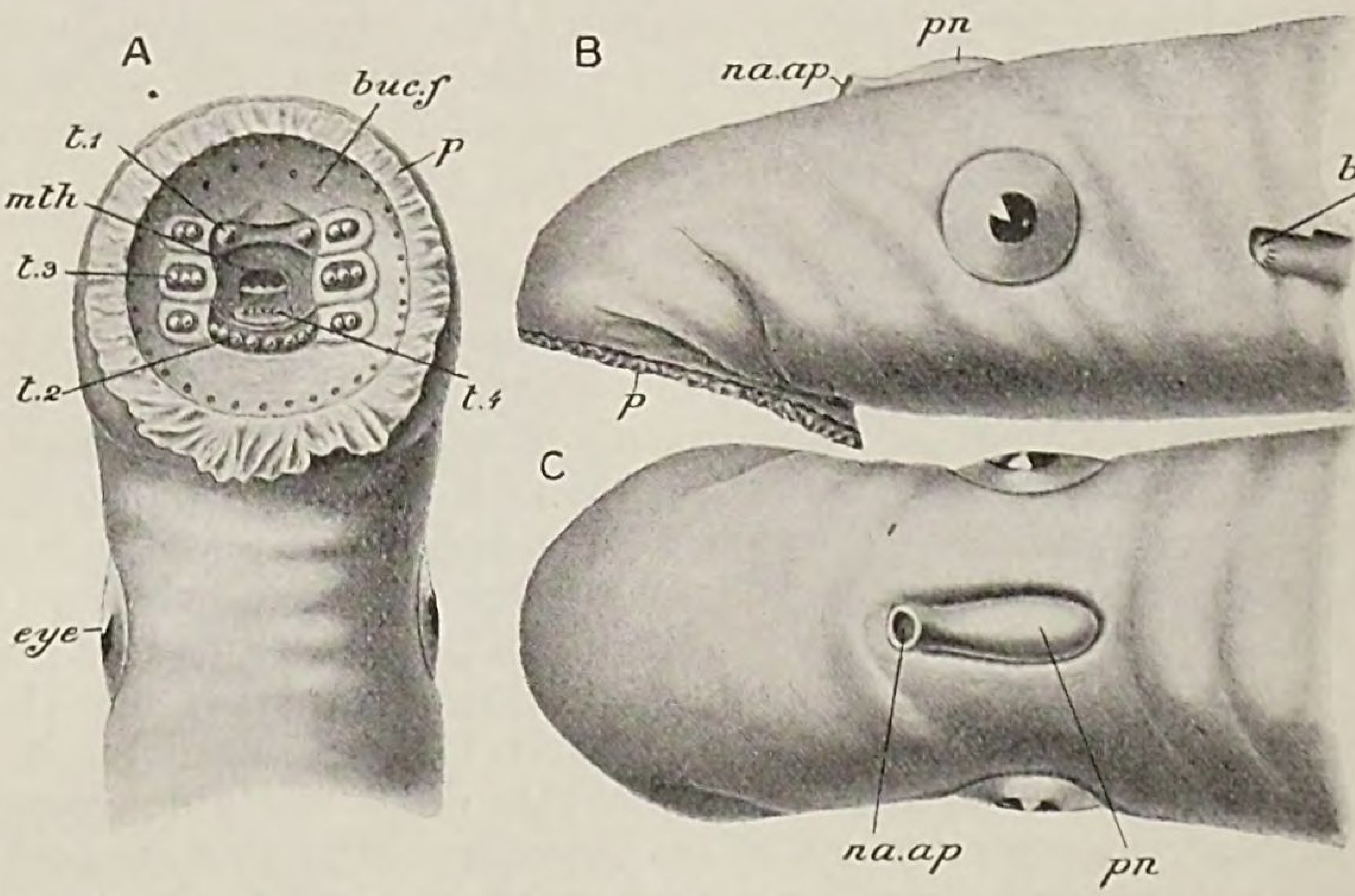


FIG. 749.—**Petromyzon marinus.** Ventral (A), lateral (B), and dorsal (C) views of the head. *br. cl. 1*, first gill-cleft; *buc. f.* buccal funnel; *eye*, eye; *mth.* mouth; *na. ap.* nasal aperture; *p.* papillæ; *pn.* pineal area; t^1. t^2. t^3. teeth of buccal funnel; t^4. teeth of tongue. (After W. K. Parker.)

side to side. At the anterior end, and directed downwards, is a large basin-like depression, the *buccal funnel* (*buc. f.*), surrounded with papillæ (*p.*) and beset internally with yellow, horny *teeth* (t^1—t^3). At the bottom of the funnel projects the end of the *tongue* (t^4), also bearing teeth, and having immediately above it the narrow *mouth* (*mth.*). On the dorsal surface of the head is the single median *nostril* (*na. ap.*), and immediately behind it a transparent area of skin (*pn.*) indicates the position of the pineal organ. The paired eyes have no eyelids, but are covered by a transparent area of skin. The gill-slits (*br. cl. 1*) are seven pairs of small apertures on the sides of the head, the first a little behind the eyes. On the ventral surface, marking the junction between trunk and

tail, is the very small *anus* (Fig. 758, *a.*), lying in a slight depression and having immediately behind it a small papilla pierced at its extremity by the *urinogenital aperture* (*z.*). It has been suggested that a pair of ridges, lying one on each side of the anus, represent vestiges of pelvic fins; otherwise there is no trace of paired appendages. Two dorsal fins and a caudal fin are present, the second dorsal being continuous with the caudal.

Lampreys live on small Crustacea, Worms, and other aquatic organisms, but also prey upon Fishes, attaching themselves to the bodies of the latter by the sucker-like mouth, and rasping off their flesh with the armed tongue. They are often found holding on to stones by the buccal funnel, and under these circumstances perform regular respiratory movements, the branchial region expanding and contracting like the thorax of a Mammal. The

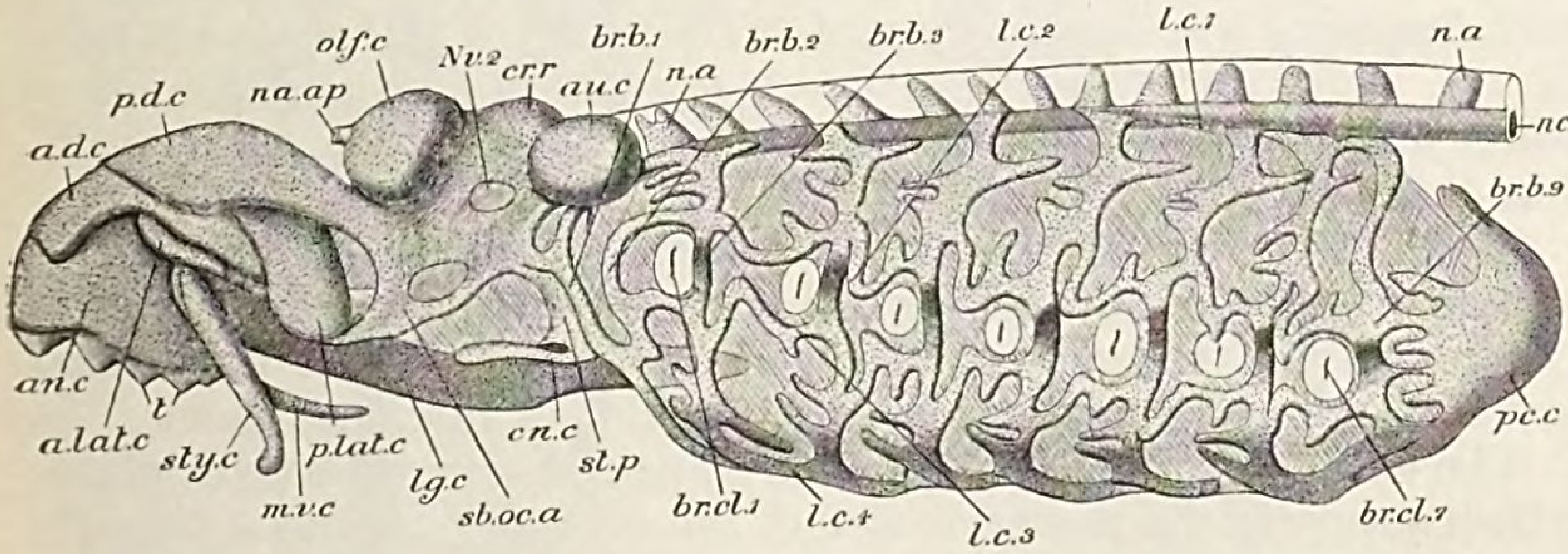


FIG. 750.—**Petromyzon marinus.** Skull, with branchial basket and anterior part of vertebral column. The cartilaginous parts are dotted. *a. d. c.* anterior dorsal cartilage; *a. lat. c.* anterior lateral cartilage; *an. c.* annular cartilage; *au. c.* auditory capsule; *br. b. 1—7*, vertical bars of branchial basket; *br. cl. 1—7*, external branchial clefts; *cn. c.* cornual cartilage; *cr. r.* cranial roof; *l. c. 1—4*, longitudinal bars of branchial basket; *lg. c.* lingual cartilage; *m. v. c.* median ventral cartilage; *na. ap.* nasal aperture; *nch.* notochord; *Nv. 2*, foramen for optic nerve; *olf. c.* olfactory capsule; *pc. c.* pericardial cartilage; *p. d. c.* posterior dorsal cartilage; *p. lat. c.* posterior lateral cartilage; *sb. oc. a.* sub-ocular arch; *st. p*, styloid process; *sty. c.* styliform cartilage; *t.* teeth. (After W. K. Parker.)

reason of this is that when the animal is adhering by the mouth the respiratory current cannot take its usual course—entering at the mouth and leaving by the gill-slits—but is pumped by muscular action both into and out of the branchial apertures.

The *skin* is soft and slimy, mottled greenish-brown in P. marinus, bluish above and silvery on the sides in the fresh-water species. The epiderm contains unicellular glands, the secretion of which gives its slimy character to the skin. The segmental sense organs take the form of a double *lateral line* and of minute pits on the head. There is no trace of exoskeleton.

Skeleton.—The *axial skeleton* of the trunk is very simple. There is a persistent notochord (Fig. 750, *nch.*) with a tough sheath composed of an inner fibrous and an outer elastic layer. Attached to the sides of the notochord are little vertical rods of cartilage (*n. a.*) arranged segmentally and bounding the spinal

canal on each side: they are rudimentary neural arches. For the rest of its extent the spinal canal is enclosed only by tough, pigmented connective tissue.

The *cranium* also exhibits a very primitive type of structure. Its floor is formed by a *basal plate* (Fig. 751, *b. pl.*), made by the union of the parachordals and trabeculæ, and surrounding posteriorly the fore-end of the notochord. Immediately in front of the termination of the notochord is a large aperture, the *basi-cranial fontanelle* (*b. cr. f.*), due to the non-union of the posterior ends of the trabeculæ; through it passes the pituitary pouch, presently to be referred to (Fig. 754), on its way from the olfactory sac to the ventral surface of the notochord. Lateral walls extend upwards from each side of the basal plate, but the roof of the cranium is formed by membrane except at one point, where a narrow transverse bar (*cr. r.*) extends across between the side-walls and furnishes a rudimentary roof. United with the posterior end of the basal plate are the *auditory capsules* (*au. c.*), and the side-walls are pierced with apertures for the cerebral nerves (*Nv. 2*, *Nv. 5*, *Nv. 8*.).

So far the skull is thoroughly typical, though in an extremely simple or embryonic condition; the remaining parts of it differ a good deal from the ordinary structure as described in the preceding section, and are in many cases very difficult of interpretation.

The *olfactory capsule* (*olf. c.*) is an unpaired concavo-convex plate which supports the posterior wall of the olfactory sac and is pierced by paired apertures for the olfactory nerves. It is unique in being united to the cranium by fibrous tissue only.

Extending outwards and downwards from each side of the basal plate is an inverted arch of cartilage, called the *sub-ocular arch* (Figs. 750 and 751, *sb. oc. a.*), from the fact that it affords a support to the eye. From its posterior end a slender *styloid process* (*st. p.*) passes directly downwards and is connected at its lower end with a small *cornual cartilage* (*cn. c.*). In all probability the sub-ocular arch answers to the palato-quadrate or primary upper jaw, the styloid and cornual cartilages to the main part of the hyoid arch. In close relation with the angle of the sub-ocular arch is an upwardly directed plate, the *posterior lateral cartilage* (*p.lat.c.*), which probably answers to the primary lower jaw, or Meckel's cartilage.

Connected with the anterior end of the basal plate is the large bilobed *posterior dorsal cartilage* (*p. d. c.*); it appears to be formed from the united anterior ends of the trabeculæ. Below and projecting in front of it is the *anterior dorsal cartilage* (*a. d. c.*), which is probably homologous with the upper labial cartilage of some Fishes and Amphibia (see below). Also belonging to the series of labial cartilages are the paired *anterior lateral cartilages* (*a. l. c.*) and the great ring-shaped *annular cartilage* (*an. c.*) which supports the edge of the buccal funnel.

The tongue is supported by a long unpaired *lingual cartilage* (Fig. 750, *lg. c.*), which probably answers to the basi-hyal or

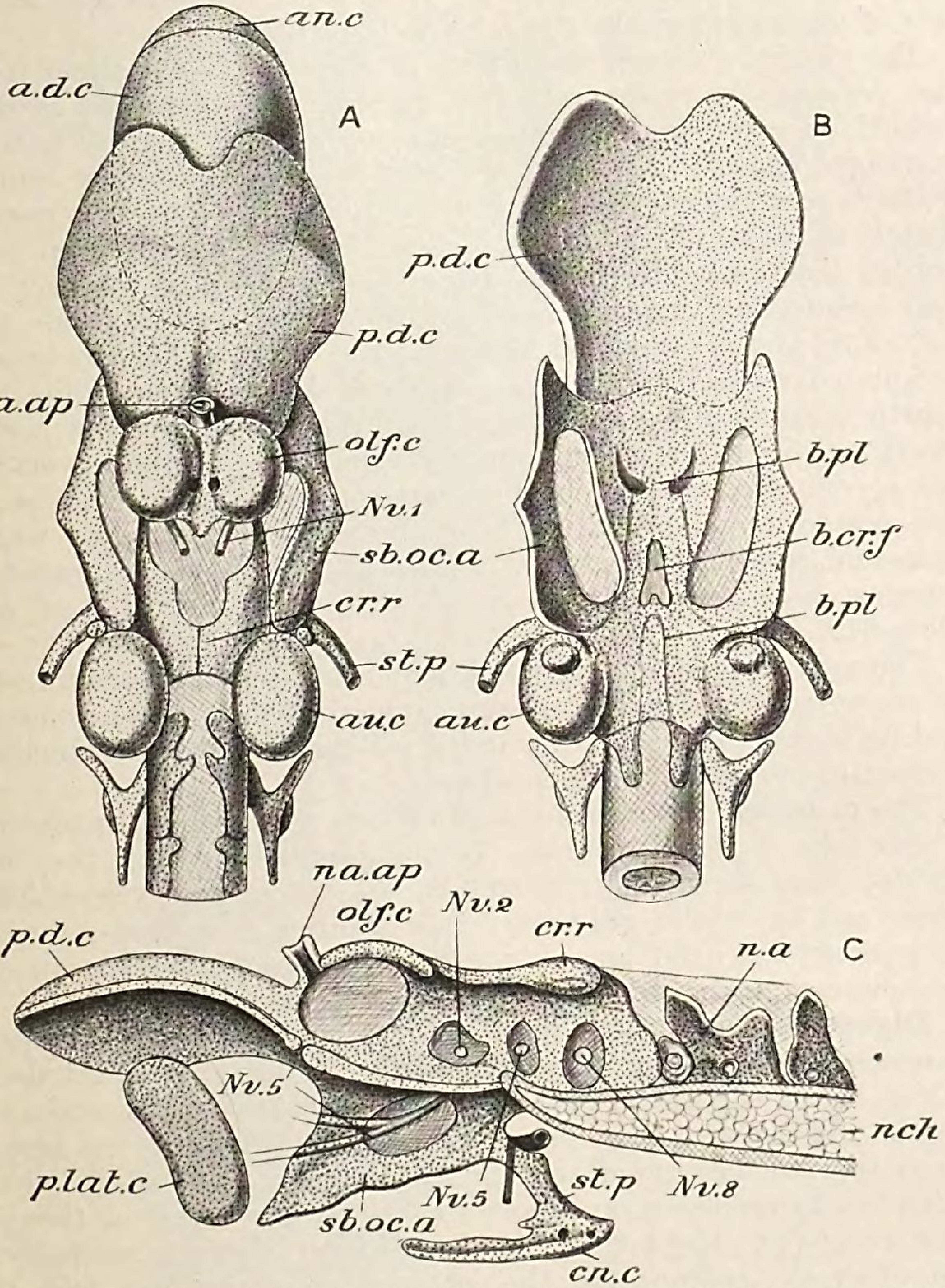


FIG. 751.—**Petromyzon marinus.** Dorsal (A), ventral (B), and sectional (C), views of skull. The cartilaginous parts are dotted. *a. d. c.* anterior dorsal cartilage; *an. c.* annular cartilage; *au. c.* auditory capsule; *b. cr. f.* basi-cranial fontanelle; *b. pl.* basal plate; *cn. c.* cornual cartilage; *cr. r.* cranial roof; *na. ap.* nasal aperture; *nch.* notochord; *Nv. 1*, olfactory nerve; *Nv. 2, 5*, and *8*, foramina for the optic, trigeminal, and auditory nerves; *Nv. 5'*, fifth nerve; *olf. c.* olfactory capsule; *p. d. c.* posterior dorsal cartilage; *p. lat. c.* posterior lateral cartilage; *sb. oc. a.* sub-ocular arch; *st. p.* styloid process. (After W. K. Parker.)

median ventral element of the hyoid arch of other Craniata (see p. 71); it is tipped in front by a small median and a pair of still smaller lateral cartilages. Below it is a slender T-shaped *median*

ventral cartilage (*m. v. c.*), which may possibly be the median ventral element of the mandibular arch. Lastly, attached to each side of the annular cartilage and passing backwards and downwards, are a pair of tapering, rod-like *styliform cartilages* (*sty. c.*).

The visceral skeleton also differs in a remarkable manner from the ordinary craniate type. It consists of a *branchial basket*, formed, on each side, of nine irregularly curved vertical bars of cartilage (Fig. 750, *br. b. 1—9*), the first placed almost immediately posterior to the styloid cartilage, the second immediately in front of the first gill-cleft, the remaining seven just behind the seven gill-clefts. These bars are united together by four longitudinal rods (*lc. 1—4*), of which one lies alongside the notochord and is connected in front with the cranium, two others are placed respectively above and below the gill-clefts, while the fourth is situated close to the middle ventral line and is partly fused with its fellow of the opposite side. The posterior vertical bar is connected with a cup-like cartilage (*pc. c.*), which supports the posterior and lateral walls of the pericardium. The whole branchial basket lies external to the gill-pouches and branchial arteries, not, like typical visceral arches, in the walls of the pharynx.

The median fins are supported by delicate cartilaginous fin-rays or *pterygiophores*, which are more numerous than the myomeres, and lie parallel to one another in the substance of the fin, extending downwards to the fibrous neural tube.

The **muscles** of the trunk and tail are arranged in myomeres which take a zigzag course. In the branchial region they are divided into dorsal and ventral bands which pass respectively above and below the gill-slits. A great mass of radiating muscle is inserted into the buccal funnel, and the tongue has an extremely complex musculature.

Digestive Organs.—The *teeth* are laminated horny cones: beneath them lie mesodermal papillæ covered with ectoderm which bear a superficial resemblance to the germs of true calcified teeth. The mouth leads into a *buccal cavity* (Fig. 752, *m.*) formed from the stomodæum of the embryo, and communicating behind with two tubes placed one above the other: the dorsal of these is the *gullet* (*œs.*), the ventral the *respiratory tube* (*r. t.*, see below): guarding the entrance to the latter is a curtain-like fold, the *velum* (*vl.*). The gullet bends over the pericardium and enters the intestine (*int.*) by a valvular aperture. The *intestine* passes without convolutions to the anus: its anterior end is slightly dilated and is the only representative of a stomach: its posterior end is widened to form the *rectum* (Fig. 758, *r.*). The whole of the intestine is formed from the mesenteron of the embryo, and the blastopore becomes the anus, there being no proctodæum. The lumen of the intestine is semilunar, owing to the presence

of a *typhlosole* (Fig. 757, *int.*), which takes a somewhat spiral

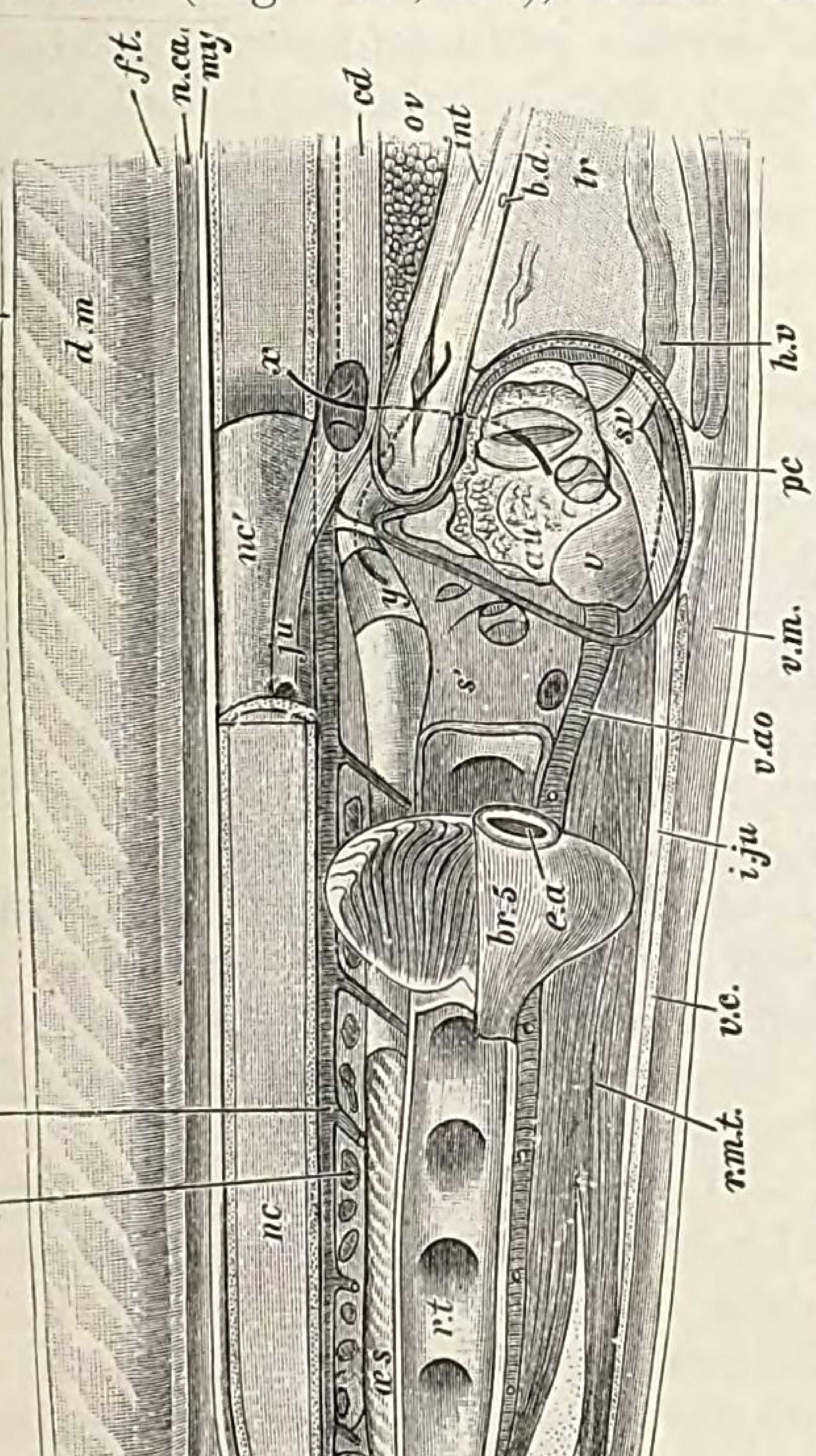


FIG. 752.—**Petromyzon marinus.** Dissection of female. The cartilaginous parts and the sheath of the notochord are dotted. *a. d.* anterior dorsal cartilage; *an.* annular cartilage; *au.* auricle, opened to show the auriculo-ventricular aperture below and the sinu-auricular above; *b. d.* aperture of bile-duct (abnormal); *b. p′.* portion of basal plate behind basi-cranial fontanelle; *br.* brain; *br. 5*, fifth left gill-sac, the upper half cut open; *cd*, left cardinal vein; *d. ao.* dorsal aorta; *d. m.* dorsal muscles; *e. a.* external aperture of fifth gill-sac; *f. t.* fibrous tissue of neural canal; *gr.* groove below buccal funnel; *h. p.* portion of basal plate anterior to basi-cranial fontanelle; *h. v.* hepatic vein; *i.* integument; *i. ju.* inferior jugular vein; *int.* intestine; *ju.* jugular vein; *lg.* lingual cartilage; *lg′.* small cartilage attached to lingual; *lr.* liver; *m*, buccal cavity; *mv.* median ventral cartilage; *my*, spinal cord; *na*, olfactory sac; *na′*, pituitary pouch; *na″.* nasal aperture; *na. c.* nasal capsule; *nc.*, *nc′.* notochord; *n. ca.* spinal canal; *oc*, cranial roof; *æs*, gullet; *o. f.* buccal funnel; *ov.* ovary; *pc.* pericardium; *p. d.* posterior dorsal cartilage; *p. m. t.* protractor muscle of tongue; *r. m. t.* retractor of tongue; *r. m. t′.* its tendon; *r. t.* respiratory tube; *s*, *s′*, lymph sinus surrounding gullet; *s. v.* sinus venosus; *t. t′.* tongue; *v.* ventricle; *v. ao.* ventral aorta; *v. c.* ventral longitudinal bar of branchial basket; *vl.* velum; *v. m.* ventral muscles; *x*, bristle passed from cardinal vein through sinus venosus into auricle; *y*, bristle passed from gullet into intestine. (From Parker's *Zootomy.*)

course and is hence known as the *spiral valve.* There is no continuous mesentery, but a number of narrow supporting bands.

The *liver* (Fig. 752, *lr.*) is a large one-lobed organ, and is peculiar from the fact that there is neither gall-bladder nor bile-duct in the adult, except as an individual variation, although both are present in the larva. There is a small gland opening into the intestine which may represent a *pancreas*: the *spleen* is absent. Paired glands imbedded in the muscles of the head, and opening into the mouth, are known as "*salivary glands.*"

Respiratory Organs.—The Lampreys differ from all other Vertebrata in the fact that the gills do not open directly into the enteric canal in the adult, but into a *respiratory tube* (Fig. 752, *r.t.*) lying below the gullet. This is a wide tube opening in front into the buccal cavity, and ending blindly a short distance in front of the heart: in the larva it communicates behind with the intestine, and is, in fact, the pharynx, the gullet of the adult being not yet developed; but at the time of metamorphosis it loses its connection with the intestine, and the gullet is developed as a forward extension of the latter—an entirely new formation. The respiratory organs are typical gill-pouches (*br.* 5): they have the form of biconvex lenses, and are separated from one another by wide interbranchial septa. In the larva an eighth cleft has been found in front of the first of the adult series.

Circulatory System.—The auricle (*au.*) lies to the left of the ventricle (*v.*) and receives blood from a small sinus venosus (*s. v.*). There is no conus arteriosus, but the proximal end of the ventral aorta presents a slight dilatation or *bulbus aortæ*. Both afferent and efferent branchial arteries supply each the posterior hemibranch of one gill-pouch and the anterior hemibranch of the next; they are thus related to the gills, not to the gill-pouches. In addition to the paired jugulars (*ju.*) there is a median ventral *inferior jugular vein* (*i. ju.*) returning the blood from the lower parts of the head. There is no renal-portal system, the two branches of the caudal vein being continued directly into the cardinals (*cd.*). The red blood-corpuscles are circular nucleated discs. There is a large system of lymphatic sinuses.

Nervous System.—In the brain the small size of the *cerebellum* (Fig. 753, *crb.*) is remarkable: it is a mere transverse band roofing over the anterior end of the metacœle. The *optic lobes* (*opt. l.*) are very imperfectly differentiated, and the central region of the roof of the mid-brain is formed merely of a layer of epithelium, giving rise to an aperture (*ch. pl.* 2) when the membranes of the brain are removed, but covered in the entire organ by a vascular thickening of the pia or *choroid plexus.* On the dorsal surface of the diencephalon are two masses of nervous matter, the *ganglia habenulæ*, the right (*r. gn. hb.*) much larger than the left (*l. gn. hb.*): they are connected with the pineal apparatus. Below the diencephalon is a small flattened pituitary body (Fig. 754, *pty. b.*). In front of the diencephalon are paired bean-like masses, each con-

sisting of a small posterior portion, the *cerebral hemisphere* (*crb. h.*), and a larger anterior portion, the *olfactory lobe* (*olf. l.*). The diacœle communicates in front with a small prosocœle or common fore-ventricle, which is roofed over by a choroid plexus (*cl. pl.* 1) and from which a transverse passage goes off on each side and

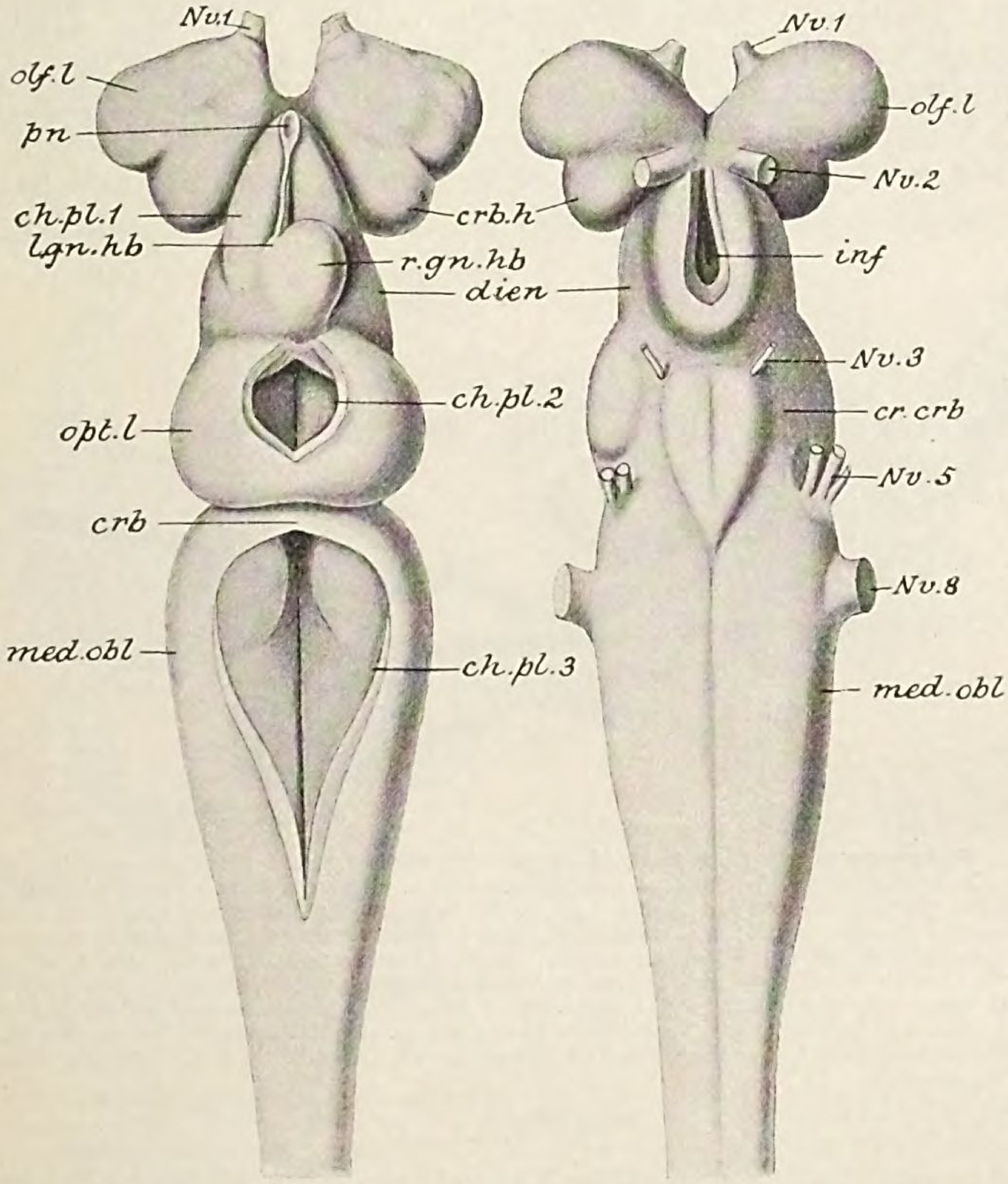


FIG. 753.—**Petromyzon marinus.** Dorsal (A) and ventral (B) views of brain. *ch. pl. 1*, anterior choroid plexus forming roof of pros- and diencephalon; *ch. pl. 2*, aperture in roof of mid-brain exposed by removal of middle choroid plexus; *ch. pl. 3*, metacœle exposed by removal of posterior choroid plexus; *crb.* cerebellum; *crb. h.* cerebral hemispheres; *cr. crb.* crura cerebri; *dien.* diencephalon; *inf.* infundibulum; *l. gn. hb.* left ganglion habenulæ; *med. obl.* medulla oblongata; *Nv. 1*, olfactory; *Nv. 2*, optic; *Nv. 3*, oculo-motor; *Nv. 5*, trigeminal, and *Nv. 8*, auditory nerves; *olf. l.* olfactory lobes; *opt. l.* optic lobes; *r. gn. hb.* right ganglion habenulæ. (After Ahlborn.)

divides into two branches, a rhinocœle going directly forwards into the olfactory lobe, and a paracœle backwards into the hemisphere.

The *pineal apparatus* consists of three vesicles placed in a vertical series: the dorsal-most of these is the vestigial *pineal eye* (Fig. 754, *pn. e.*): it has a pigmented retina, a flat and imperfectly formed lens, and is connected with the right ganglion habenulæ. The

middle vesicle (*pn.*) is in connection with the small left ganglion habenulæ. The optic nerves differ from those of the higher classes in the fact that each passes directly to the eye of its own side.

The *spinal cord* (Figs. 752 and 757, *my.*) is flattened and band-like. The dorsal roots of the spinal nerves alternate with the ventral and do not unite with them to form a trunk. There is no sympathetic. The hypoglossal is the first spinal nerve.

Sensory Organs.—The external nostril (Fig. 752, *na*,″ Fig. 754, *na. ap.*) leads by a short passage into a rounded *olfactory sac* (Fig. 752, *na*, Fig. 754) placed just in front of the brain and having its posterior wall raised into ridges covered by the olfactory or

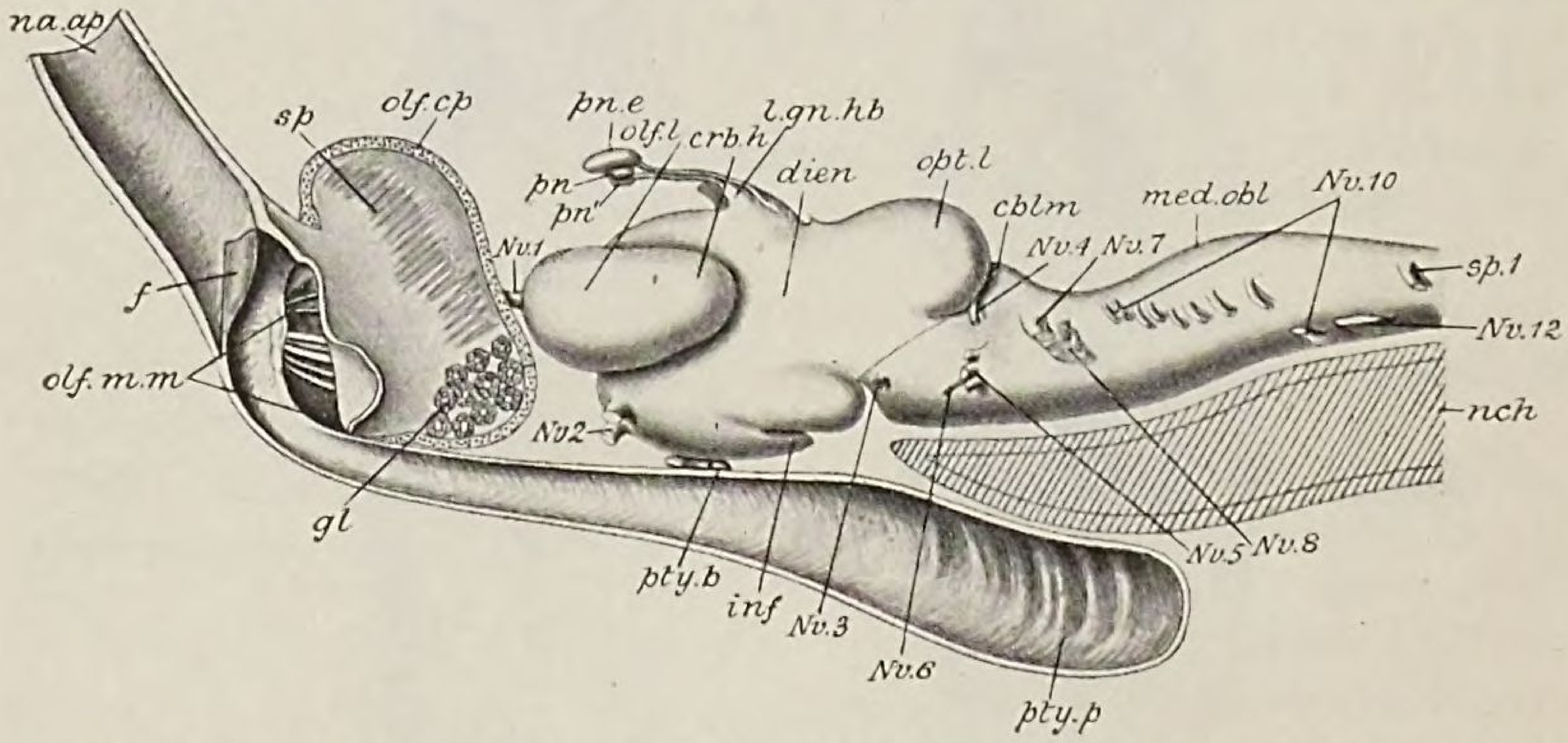


FIG. 754.—**Petromyzon.** Side view of brain with olfactory and pituitary sacs in section. *cblm.* cerebellum; *crb. h.* cerebral hemisphere; *dien.* diencephalon; *f.* fold in nasal tube; *gl.* nasal glands; *inf.* infundibulum; *l. gn. hb.* left ganglion habenulæ; *med. obl.* medulla oblongata; *na. ap.* nostril; *nch.* notochord; *Nv. 1*, olfactory nerve; *Nv. 2*, optic; *Nv. 3*, oculomotor; *Nv. 4*, trochlear; *Nv. 5*, trigeminal; *Nv. 6*, abducent; *Nv. 7*, facial; *Nv. 8*, auditory; *Nv. 10*, vagus; *Nv. 12*, hypoglossal; *olf. cp.* olfactory capsule; *olf. l.* olfactory lobe; *olf. m. m.* olfactory mucous membrane; *opt. l.* optic lobe; *pn.* middle pineal body; *pn′.* inferior pineal body; *pn. e.* pineal eye; *pty. b.* pituitary body; *pty. p.* pituitary pouch; *sp.* median septum of olfactory sac; *sp. 1*, dorsal root of first spinal nerve. (Combined from figures by Ahlborn and Kaenische.)

Schneiderian membrane (Fig. 754, *olf. m. m.*). From the bottom of the sac is given off a large *pituitary pouch* (Fig. 752, *na′*, Fig. 754, *pty. p.*) which extends downwards and backwards, between the brain and the skull-floor, passes through the basi-cranial fontanelle, and ends blindly below the anterior end of the notochord.

The relations between the olfactory sac, the pituitary pouch, and the pituitary body are very remarkable. In the embryo, before the stomodæum (Fig. 755, A, *stdm.*) communicates with the mesenteron, two unpaired ectodermal invaginations appear in front of the mouth. The foremost of these is the rudiment of the olfactory sac (*olf. s.*). The other, which is situated between the olfactory sac and the mouth, is the pituitary sac (*pty. s.*), which in this case

opens just outside the stomodæum instead of within it as in other Craniata: its inner or blind end extends to the ventral surface of the fore-brain and terminates just below the infundibulum (*inf.*). As development goes on, the olfactory and pituitary invaginations become sunk in a common pit (B), which, by the growth of the immense upper lip (*up.l.*), is gradually shifted to the top (C, D) of the head, the process being accompanied by elongation of the pituitary sac, into which the olfactory sac opens posteriorly. Where the pituitary sac comes in contact with the infundibulum it gives off numerous small follicles which become separated off and

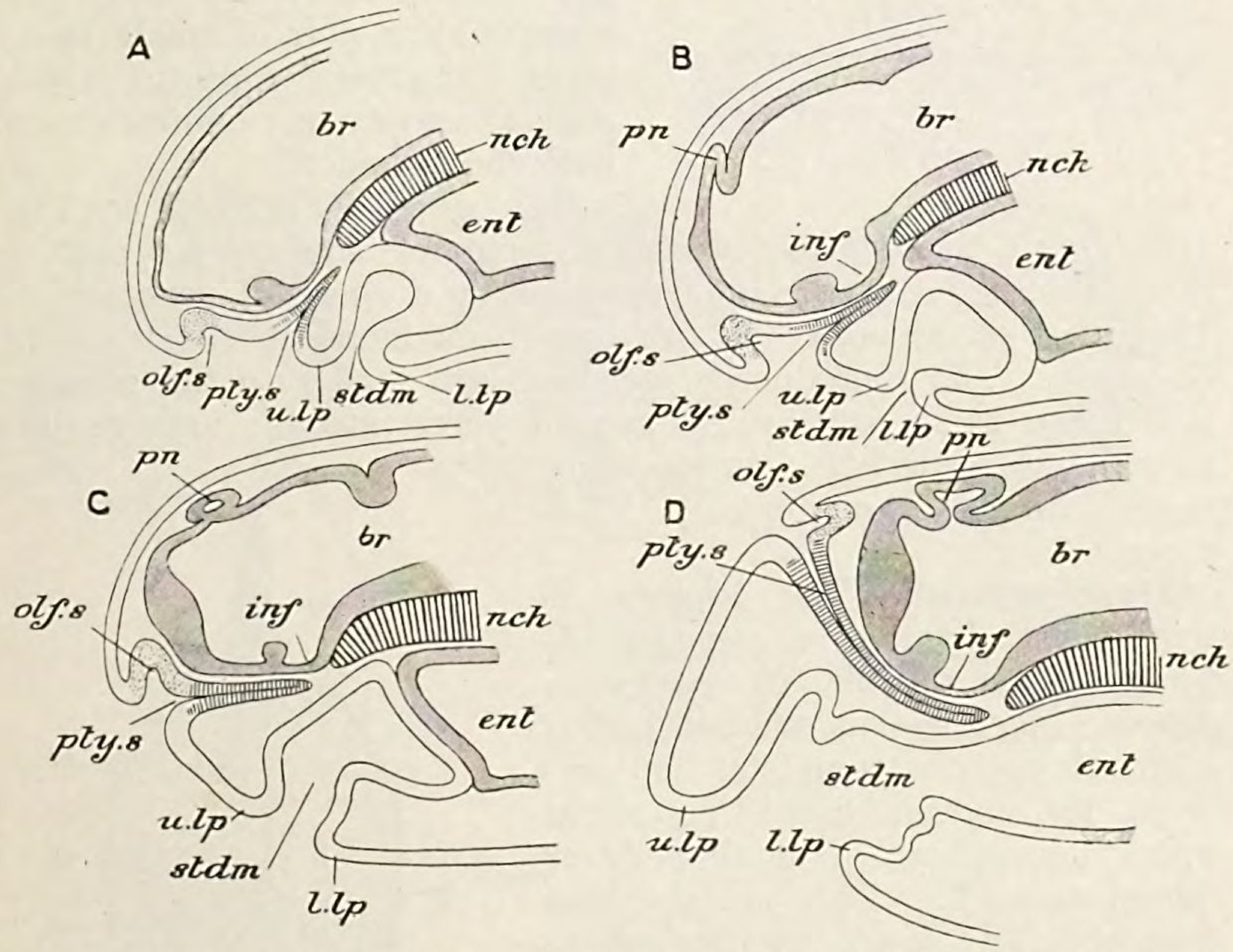


FIG. 755.—**Petromyzon.** Diagrams of four stages in the development of the olfactory and pituitary sacs. *ent.* mesenteron; *inf.* infundibulum; *l. lp.* lower lip; *nch.* notochord; *olf. s.* olfactory sac; *pn.* pineal body; *pty. s.* pituitary sac; *stdm.* stomodæum; *u. lp.* upper lip. (Altered from Dohrn.)

give rise to the pituitary body (Fig. 754, *pty. b.*). Thus the entire nasal passage of the Lamprey, including its blind pouch, is a persistent pituitary sac into which the single olfactory organ opens. Moreover, owing to the extraordinary displacement undergone during development, the pituitary sac perforates the skull-floor from above instead of from below, as in all other Craniata.

The auditory organ (Fig. 756) is remarkable for having only two semicircular canals, corresponding to the anterior (*a.s.c.*) and posterior (*p.s.c.*) of the typical organ.

Urinogenital Organs.—The *kidneys* (Figs. 757 and 758, *k.*) are long strap-shaped bodies developed from the mesonephros of the

embryo. Each is attached along one edge to the dorsal wall of the body cavity by a sheet of peritoneum; along the other or free edge runs the *ureter* (*ur.*), which is the undivided segmental duct. The ureters open posteriorly into a small *urino-genital sinus* (Fig. 758, *u.g.s.*), placed just behind the rectum, and opening, by a *urino-genital papilla* (*u.g.p.*), into a pit in which the anus (*a*) also lies. The side-walls of the sinus are pierced by a pair of small apertures, the *genital pores* (*y*), which place its cavity in communication with the cœlome.

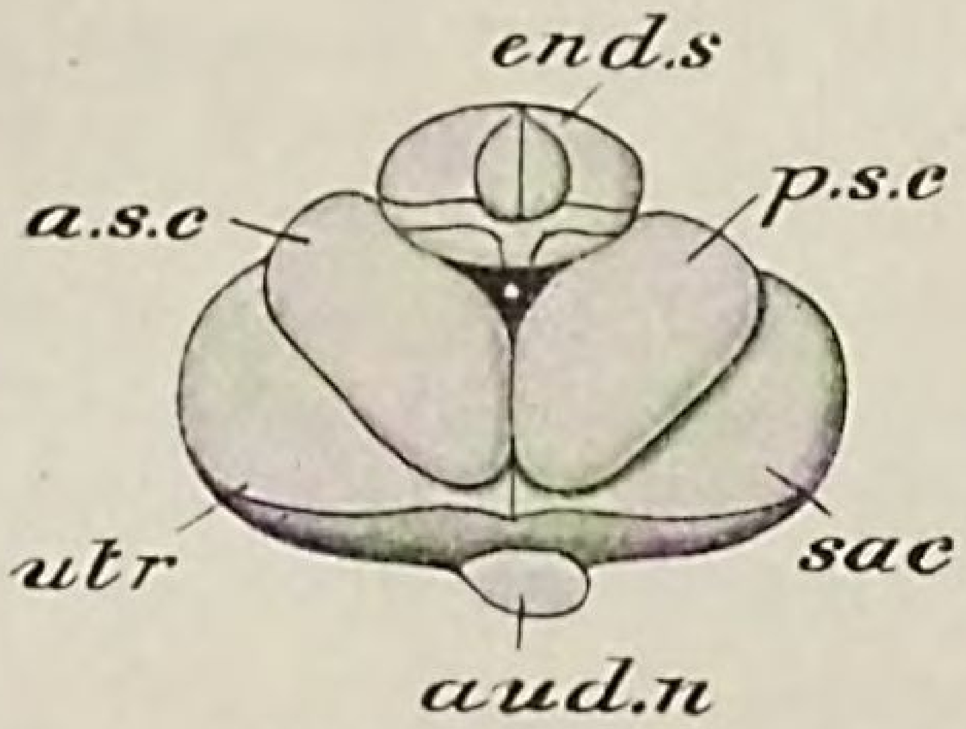


FIG. 756.—Auditory sac of **Petromyzon.** *a. s. c.* anterior semicircular canal; *aud. n.* auditory nerve; *end. s.* endolymphatic sac; *p.s.c.* posterior canal; *sac.* sacculus; *utr.* utriculus. (After Retzius.)

The *gonad* (Fig. 752, *ov*, Fig. 758, *ts*) is a large unpaired organ occupying the greater part of the abdominal cavity and suspended by a sheet of peritoneum. The sexes are separate, but ova have been found in the testis of the male. The reproductive products are shed into the cœlome and make their way by the genital pores into the urinogenital sinus, and so to the surrounding water, where impregnation takes place.

Development.—The oosperm is telolecithal, having a considerable accumulation of yolk in one hemisphere; in correspondence with this segmentation is complete but unequal, the morula consisting of an upper hemisphere of small cells or micromeres (Fig. 759, *mi. m.*), free from yolk, and of a lower hemisphere of large cells or megameres (*mg. m*), containing much yolk. In the blastula stage (D) the segmentation cavity or blastocœle (*blcl.*) is situated nearer to the upper than to the lower pole. The gastrula is not formed by invagination (E), but a cavity appears among the cells of the upper pole and becomes the archenteron, its aperture being the blastopore (C and E, *blp.*). The unsymmetrical positions of the blastocœle and archenteron are due to the comparatively rapid division of the micromeres as compared with that of the inert yolk-cells. The blastopore becomes the anus

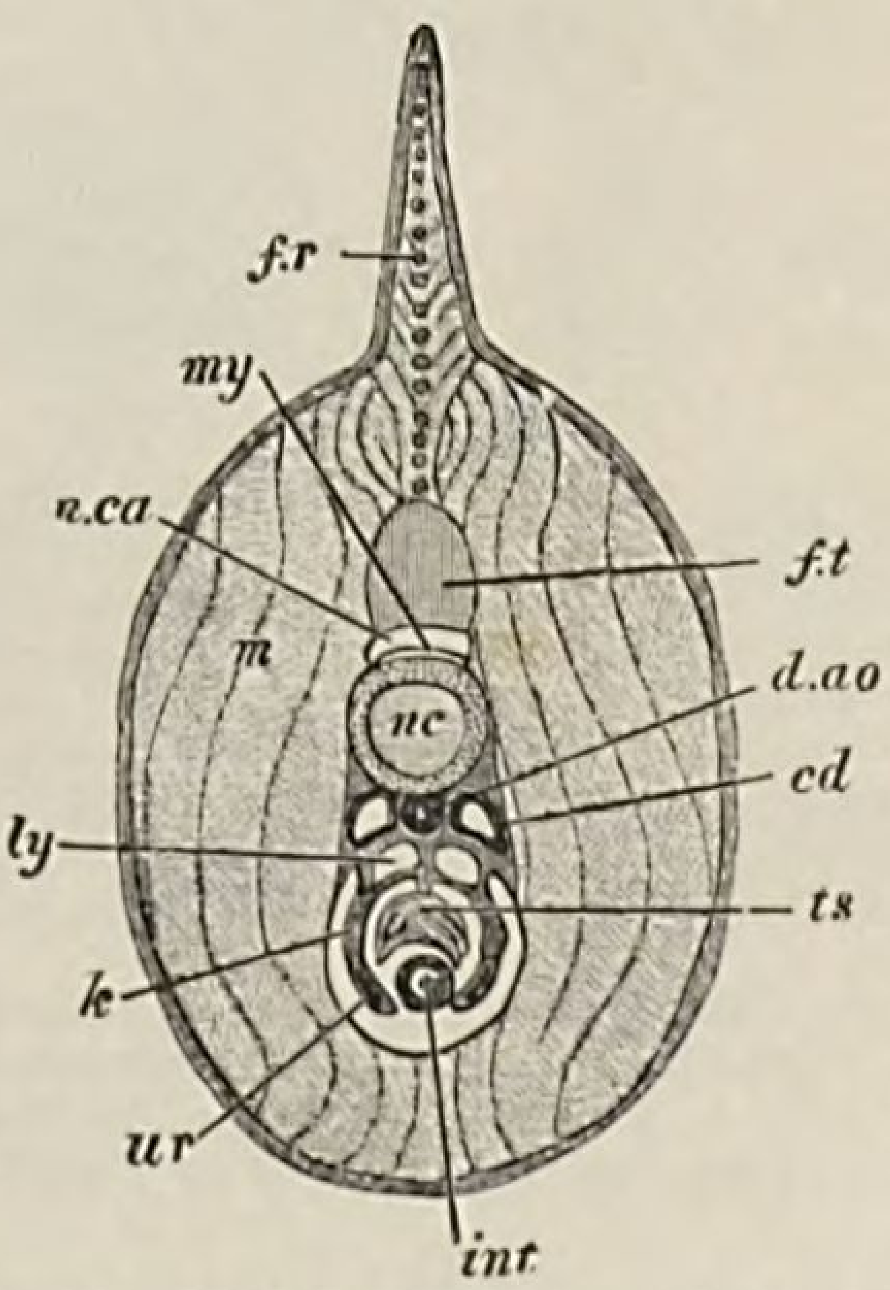


FIG. 757.—**Petromyzon marinus.** Transverse section of abdomen. *cd.* cardinal veins; *d. ao.* dorsal aorta; *f. r.* fin-rays; *f. t.* fibrous tissue of spinal canal; *int.* intestine, the line pointing to the spiral valve; *k.* kidneys; *ly.* sub-vertebral lymph sinus; *m.* body muscles; *my*, spinal cord; *nc.* notochord; *n. ca.* spinal canal; *ts.* testis; *ur.* ureter. (From Parker's *Zootomy*.)

of the adult, so that there is no proctodæum; the buccal cavity is formed from a stomodæal invagination at a comparatively late period.

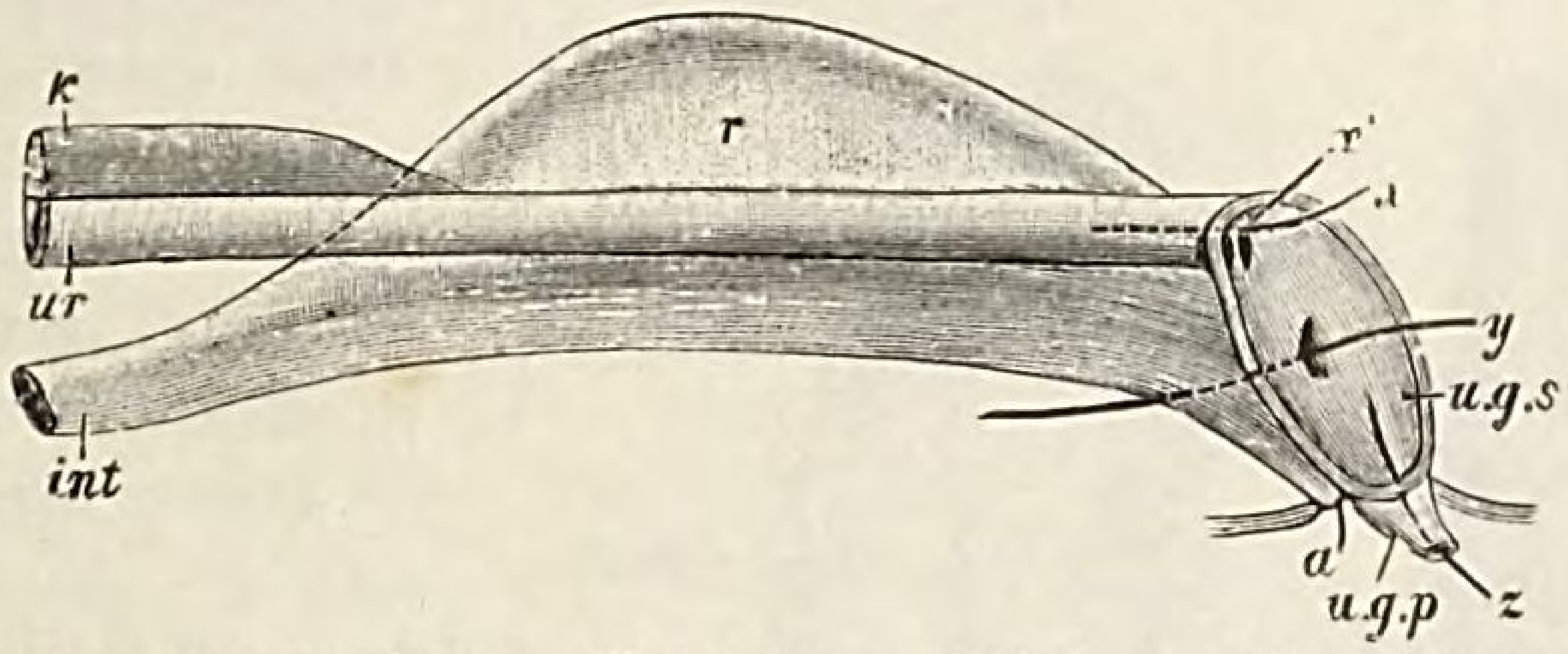


FIG. 758.—**Petromyzon marinus.** The urino-genital sinus with posterior end of intestine and part of left kidney. *a.* anus; *int.* intestine; *k.* left kidney; *r.* rectum; *u. g. p.* urino-genital papilla; *u. g. s.* urino-genital sinus; *ur.* left ureter; *x*, *x'*, apertures of ureters into urino-genital sinus; *y*, bristle passed into right genital pore; *z*, bristle passed from urino-genital aperture into sinus. (From Parker's *Zootomy*.)

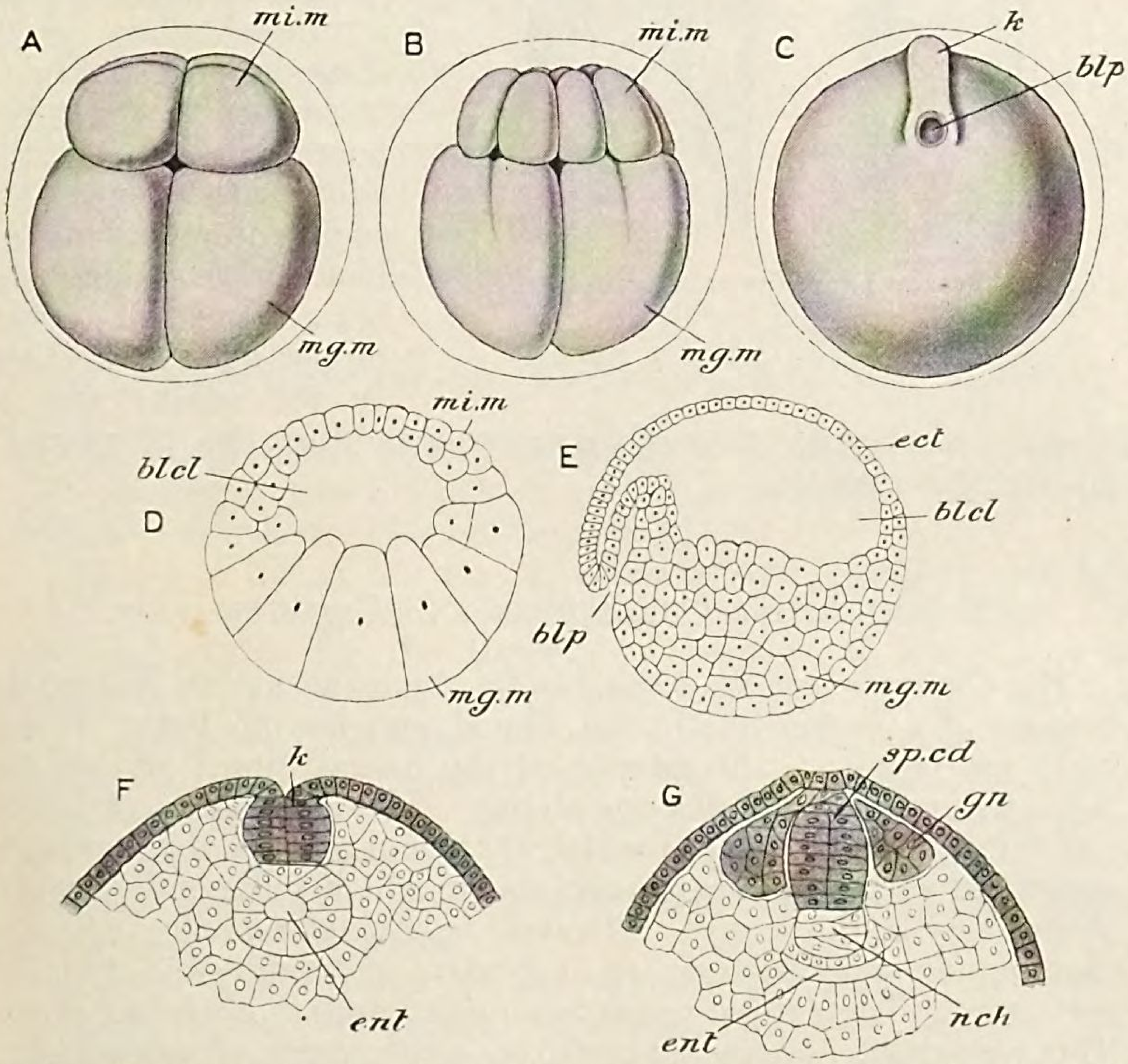


FIG. 759.—**Petromyzon.** A and B, two stages in segmentation; C, early embryo from the posterior aspect; D, section of blastula stage; E, section of gastrula stage; F, G, two stages in the development of the notochord and nervous system. *blcl.* blastocœle; *blp.* blastopore; *ect.* ectoderm; *ent.* enteron; *gn.* spinal ganglia; *k.* keel; *mg. m.* megameres; *mi. m.* micromeres; *nch.* notochord; *sp. cd.* spinal cord. (After Shipley and Kupffer.)

The formation of the nervous system is peculiar. The walls of the medullary groove are in close apposition, so that the in-growth of ectoderm, from which the brain and spinal cord are developed

has the form of a longitudinal keel devoid of a cavity; the neurocœle appears subsequently. According to some observations the ventral portion of the keel gives rise to the notochord, which is thus an ectodermal, and not, as usual, an endodermal product.

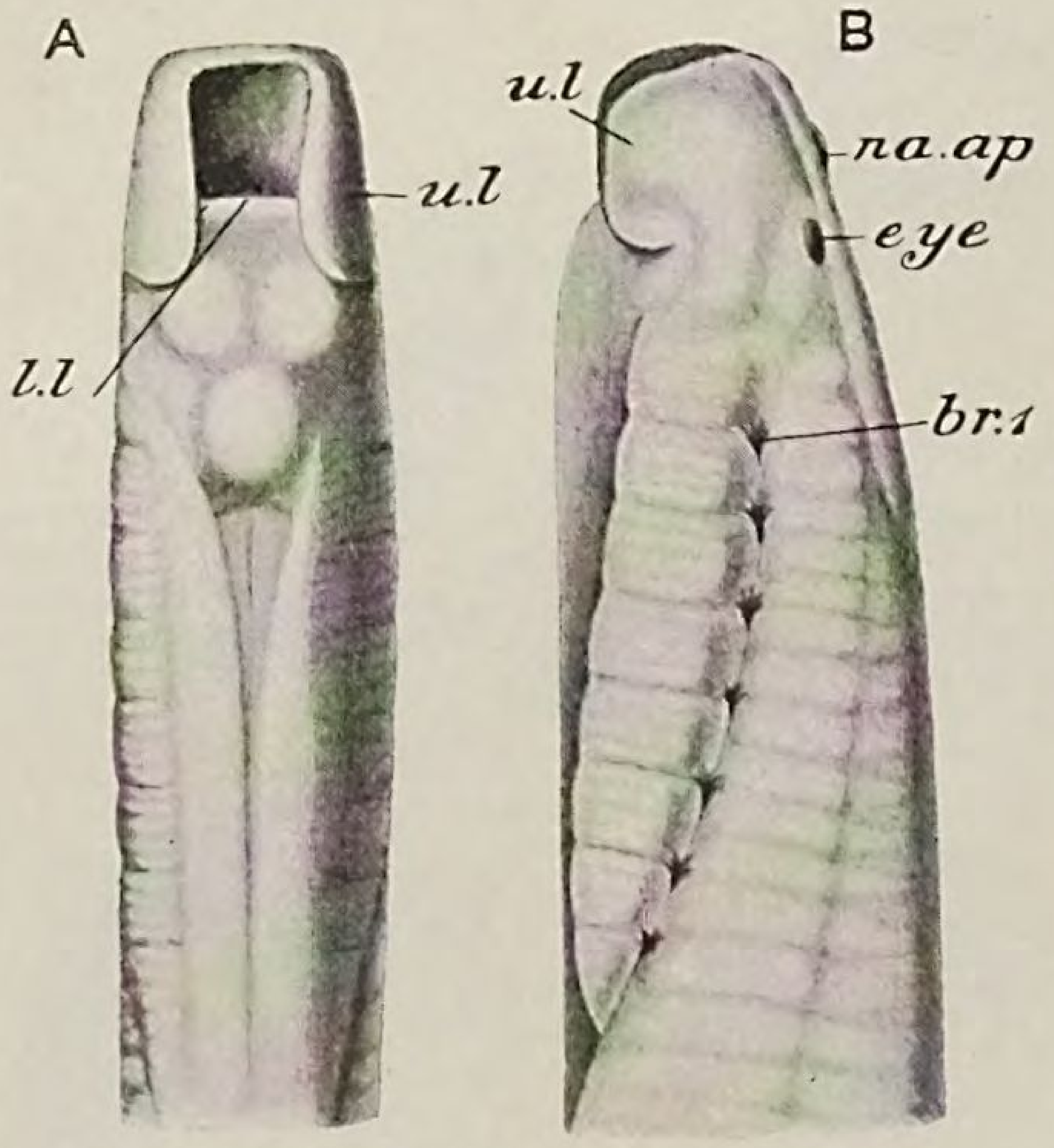


FIG. 760.—**Petromyzon fluviatilis.** Head of larva. A, from beneath; B, from the side. *br. 1*, first branchial aperture; *eye*, eye; *l. l.* lower lip; *na. ap.* nostril; *u. l.* upper lip. (After W. K. Parker.)

The young is hatched as a peculiar larval form called *Ammocœtes* (Fig. 760), which differs from the adult in several respects. It has a semicircular, hood-shaped upper lip (*u. l.*) instead of the suctorial buccal funnel of the adult; the eyes are rudimentary and hidden beneath the skin; the brain is of far greater proportional size than in the adult; and, as already mentioned, the gill-pouches open into the pharynx in the normal manner.

2. Distinctive Characters and Classification.

The Cyclostomata are Craniata, in which the mouth lies at the bottom of a sucker-like buccal funnel, and has no jaws. Horny teeth are borne on the interior of the buccal funnel and on the large tongue. Paired fins are absent. There is no exoskeleton; the skin is glandular. The vertebral column consists of a persistent notochord with a fibrous neural tube, in which rudimentary neural arches may be developed. The skull is largely or wholly roofed by membrane, and there is an extensive development of labial cartilages. The enteric canal is straight, and there is no cloaca. The respiratory organs are six or seven pairs of gill-pouches. There is no conus arteriosus and no renal portal system. There are distinct cerebral hemispheres, which may be either hollow or solid; the cerebellum is very small. Each optic nerve passes directly to the eye of its own side. The olfactory organ is single and median, but is supplied by paired olfactory nerves; it opens into a large persistent pituitary sac which perforates the basis cranii from above. The auditory organ has one or two semi-

circular canals. The kidney is a mesonephros, the ureter an archinephric duct. The gonad is unpaired, and there are no gonoducts, the genital products making their exit by genital pores.

The Class is divided into two Orders.

ORDER 1.—PETROMYZONTES.

Cyclostomata, in which there is a well-developed dorsal fin and a complete branchial basket; the pituitary sac terminates posteriorly in a blind pouch; the gills open into a respiratory tube below the gullet. This order includes the Lampreys, belonging to the genera *Petromyzon*, *Mordacia*, *Geotria*, and *Ichthyomyzon*.

ORDER 2.—MYXINOIDEI.

Cyclostomata, in which the dorsal fin is absent or feebly developed; the branchial basket is reduced to a vestige; the pituitary sac opens posteriorly into the mouth; the gills open into the pharynx in the normal manner.

This order includes the Hags or Slime-eels, belonging to the genera *Myxine* and *Bdellostoma*.

3.—COMPARISON OF THE MYXINOIDS WITH THE LAMPREY.

The organisation of the Lampreys is so uniform that all that will be necessary in the present section is to indicate the principal points in which the Hags differ from them.

Myxine is about the size of a fresh-water Lamprey—*i.e.* some forty-five cm. long: *Bdellostoma* is fully a metre in length. Both are remarkable for the immense quantities of slime they are capable of exuding from the general surface of the skin and from the segmentally arranged mucous glands. It is said that two specimens of Myxine thrown into a bucket of water are capable of gelatinising the whole with their secretion. The slime-glands of Myxine contain peculiar "thread-cells" containing a much-coiled thread which unwinds either before or after the discharge of the cell from the gland.

Myxine approaches most nearly to the condition of an internal parasite of any Vertebrate; it is said to attach itself to living Fishes and gradually to bore its way into the cœlome, devouring flesh as it goes.

The buccal funnel is edged with tentacles (Fig. 761); there is a single median tooth above the oral aperture, and two rows of smaller teeth on the tongue. The papillæ beneath the cone-like horny teeth bear a still closer superficial resemblance to rudiments (or vestiges) of true calcified teeth than is the case in the

Lamprey; but it appears that no odontoblasts and no calcified substance of any kind are formed in connection with them. The nostril (*na. ap.*) is a large unpaired aperture situated in the dorsal margin of the buccal funnel, and is continued into a passage, the pituitary sac, which opens into the pharynx. Myxine commonly lives nearly buried in mud, and the respiratory current passes through this passage to the gills.

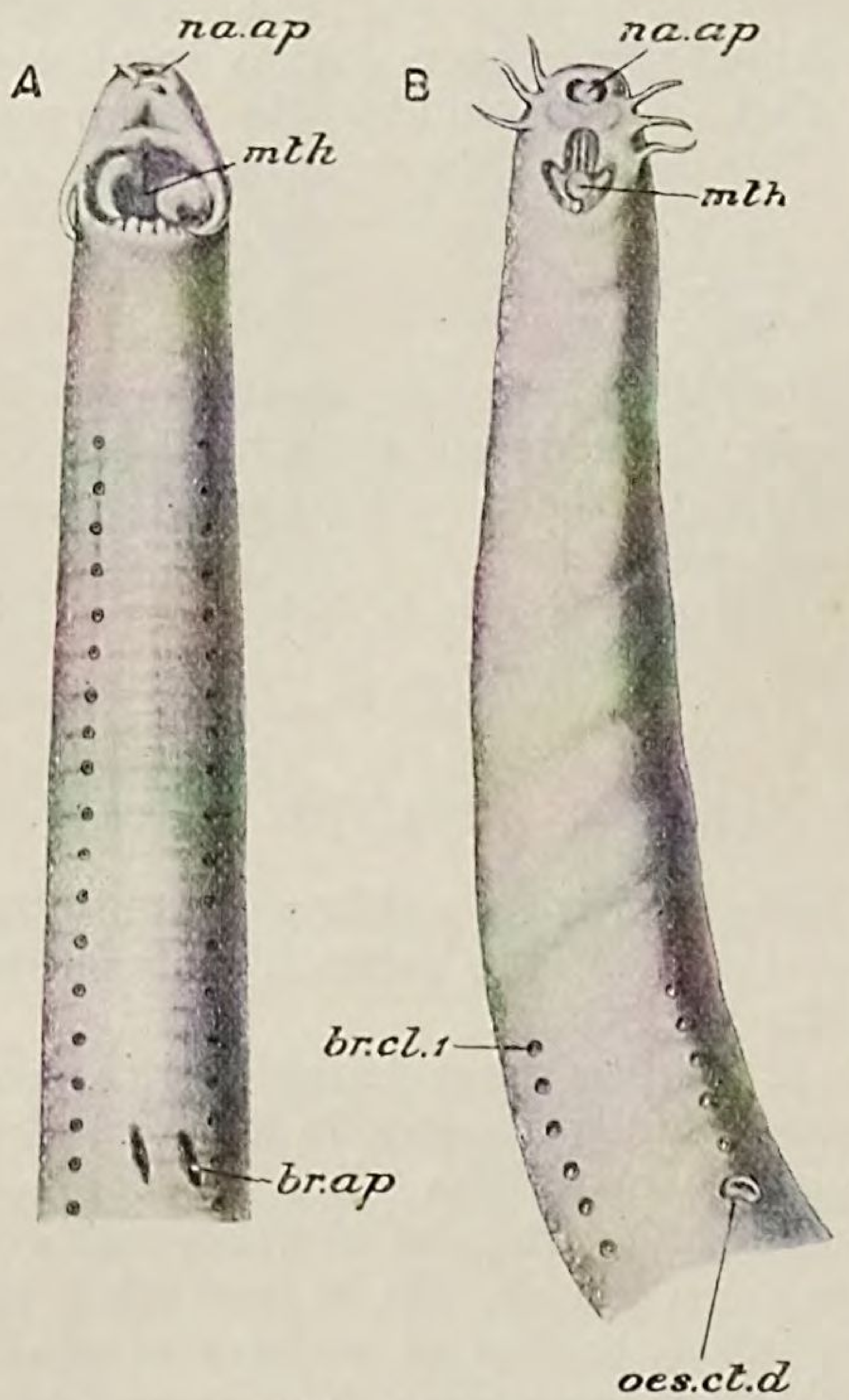


FIG. 761.—Head of **Myxine glutinosa** (A) and of **Bdellostoma forsteri** (B), from beneath. *br. ap.* branchial aperture; *br. cl. 1*, first branchial cleft; *mth.* mouth; *na. ap.* nasal aperture; *œs. ct. d.* œsophageo-cutaneous duct. The smaller openings in A are those of the mucous glands. (After W. K. Parker.)

The only fin is a narrow caudal surrounding the end of the tail. The respiratory organs present striking differences in the two genera. In Bdellostoma there are six or seven very small external branchial apertures (*br. cl.* 1) on each side. Each communicates by a short tube with one of the gill-pouches, which is again connected with the pharnyx by another tube. Behind and close to the gill-slit, on the left side, is an aperture leading into a tube, the *œsophageo-cutaneous duct* (*œs. ct. d.*), which opens directly into the pharynx. In Myxine (Fig. 762) the tubes leading outwards from the gill-pouches all unite together before opening on the exterior, so that there is only a single external branchial aperture (*br. ap.*) on each side; into the left common tube (*c. br. t.*) the œsophageo-cutaneous duct (*œs. ct. d.*) opens. In both genera the internal branchial apertures communicate directly with the pharynx; there is no respiratory tube.

The neural canal is over-arched merely by fibrous tissue (Fig. 762, *nt.*); there is no trace even of the rudimentary neural arches of the Lamprey. Similarly the roof of the skull is entirely membranous. The nasal passage (*na. t.*) is strengthened by rings of cartilage, and the buccal tentacles are supported by rods of the

same tissue. Behind the styloid cartilage or hyoid bar (*st. p.*) is a rod connected below with the subocular arch; it probably represents the first branchial bar. The tongue is supported by an immense cartilage (*m.v.c.*), which probably represents the small median ventral cartilage of the Lamprey (Fig. 750, *m.v.c.*). The branchial basket is quite rudimentary, being represented only by a small irregular cartilage in the walls of the œsophageo-cutaneous duct, and, in Myxine, by a smaller cartilage (Fig. 762, *br. b.*) on the right side supporting the common external gill-tube.

The intestine is very wide. The liver consists of two separate portions, the ducts of which unite to form a common bile duct: a gall-bladder is present. The brain differs considerably from that of the Lamprey, especially in the larger hemispheres, absence of lateral ventricles, and smaller mid-brain. The eyes are vestigial and sunk beneath the skin, and the auditory organ (Fig. 763) has only a single semicircular canal, which, having an ampulla at each end, probably represents both anterior and posterior canals.

Bdellostoma has a persistent pronephros in the form of a paired irregularly ovoidal body situated just above the heart: the nephrostomes open into the pericardium. The functional kidney is the mesonephros, and is specially interesting from the fact that it retains in the adult its primitive segmental arrangement. The ureter (archi-

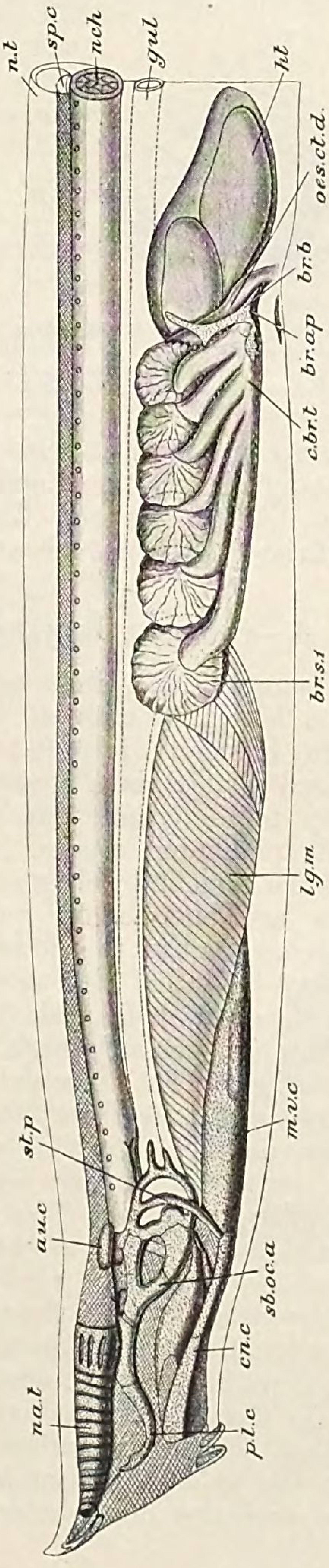


FIG. 762.—Dissection of **Myxine glutinosa** from the left side. *au. c.* auditory capsule; *br. ap.* left branchial aperture; *br. b.* rudiment of branchial basket; *br. s. 1*, first gill-sac; *c. br. t.* common branchial tube; *cn. c.* cornual cartilage; *gul.* gullet; *ht.* heart; *lg. m.* lingual muscles; *m. v. c.* median ventral cartilage; *na. t.* nasal tube; *nch.* notochord; *n. t.* neural tube; *œs. ct. d.* œsophageo-cutaneous duct; *pl. c.* posterior lateral cartilage; *sb. oc. a.* subocular arch; *sp. c.* spinal cord; *st. c.* styloid process. (After W. K. Parker, modified from Burn.)

nephric duct, Fig. 764, *a*) sends off in each segment a coiled tubule (*b*) or nephridium, with a single Malpighian capsule (*c*), into which a branch from the aorta (*d*) enters and forms a glomerulus.

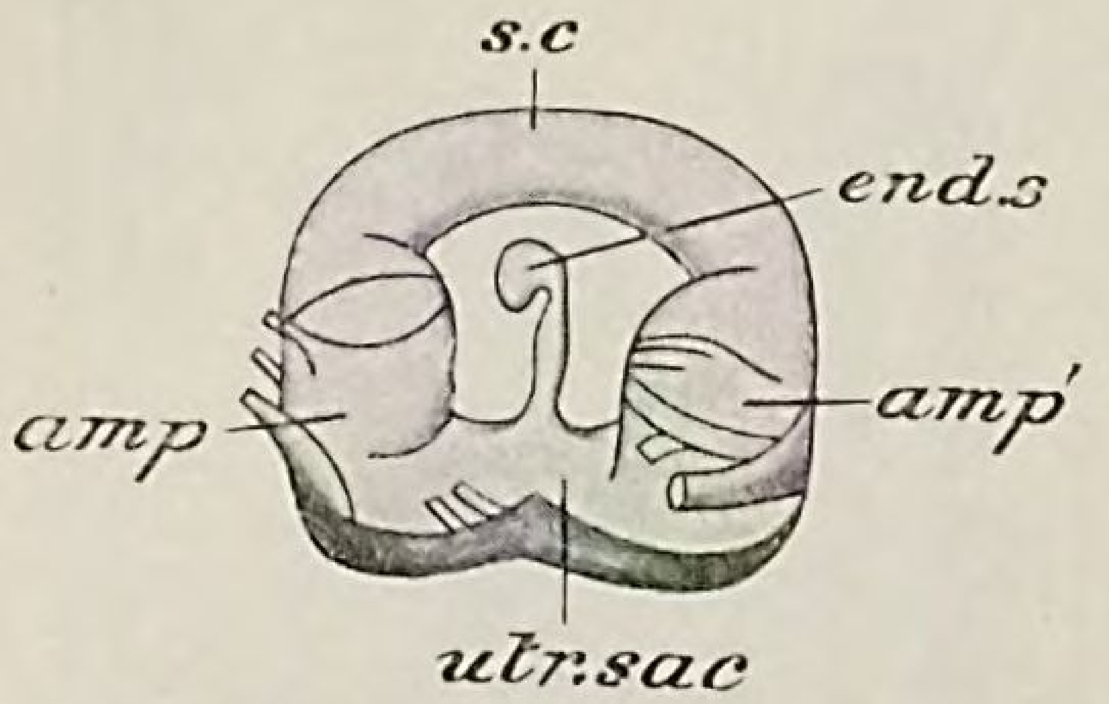


FIG. 763.—Auditory organ of **Myxine.** *amp., amp.'* ampullæ; *end. s.* endolymphatic sac; *s. c.* semicircular canal; *utr. sac.* utriculo-sacculus. (After Retzius.)

Myxine is hermaphrodite and protandrous—*i.e.*, the gonad of the young animal produces sperms, and at a later period gives rise to ova. The eggs of both genera are of great proportional size, and those of Myxine are enclosed when laid in a horny shell bearing numerous hooked processes at each pole: by means of these the eggs are entangled together, and probably also attached to seaweed. The development of the Hags is not known.

4.—General Remarks.

The Lampreys and Hags are undoubtedly the lowest of craniate Vertebrata, but are in many respects so highly specialised that it is a matter of great difficulty to determine their affinities with the remaining classes. The structure of the vertebral column and of the cranium are undoubtedly primitive in the extreme; but in the development of what may be called the accessory portions of the skull, such as labial cartilages, they show a singularly high degree of specialisation. The branchial basket is quite *sui generis*, the theory that its vertical bars are true branchial arches, displaced outwards during development, being quite unproved. The absence of functional jaws is very remarkable, seeing that in the remaining Craniata these structures always bound the mouth at a period when the skull is in the stage of development in which it remains permanently in Cyclostomes: it is quite possible that their functionless condition may be due to degeneration accompanying the evolution of a suctorial mouth.

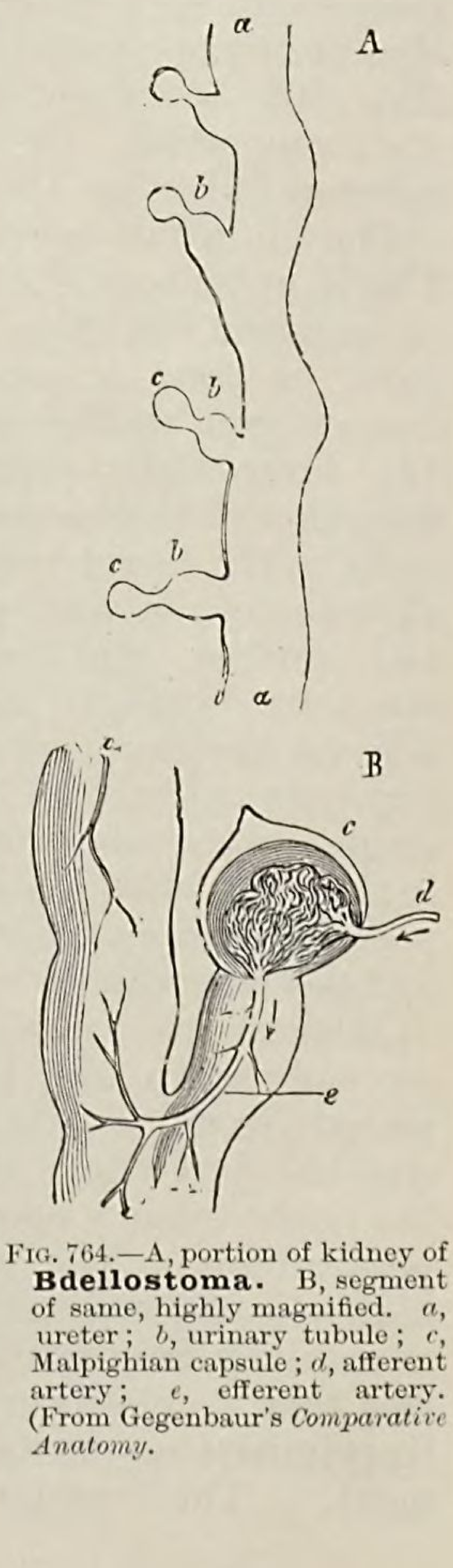


FIG. 764.—A, portion of kidney of **Bdellostoma.** B, segment of same, highly magnified. *a*, ureter; *b*, urinary tubule; *c*, Malpighian capsule; *d*, afferent artery; *e*, efferent artery. (From Gegenbaur's *Comparative Anatomy*.)

The brain, in spite of its small size, is in some respects—notably in the presence of cerebral hemispheres—of a more advanced type than that of some of the true Fishes. The circumstance that the pituitary pouch perforates the skull-floor from above and becomes early associated with the olfactory sac, is unique among the Vertebrata. The kidney of Bdellostoma is of the most primitive type, and the presence of a large pronephros is a significant archaic character. The total absence of limbs may be a result of degeneration.

The geographical distribution of the class is interesting from the fact that each order contains some genera which are mainly northern, others which are exclusively southern. Petromyzon is found on the coasts and in the rivers of Europe, North America, Japan, and West Africa; it is therefore mainly Holarctic. Ichthyomyzon is found on the western coasts of North America, Mordacia in Tasmania and Chili, Geotria in the rivers of Chili, Australia, and New Zealand. Myxine occurs in the North Atlantic and on the Pacific Coast of South America; Bdellostoma on the coasts of South Africa, New Zealand, and Chili.

Until quite recently no undoubted fossil remains of Cyclostomes have been known, but there is some reason to believe that a little fossil fish, *Palæospondylus gunni* (Fig. 765), lately discovered in the Devonian rocks of Scotland, is referable to this class. It is about an inch long and shows two regions, the cranium and the vertebral column; there is no trace of jaws, branchial basket, or limbs. The vertebral column is composed of calcified centra with neural arches; hæmal arches are present in the caudal region; the structure of this part of the skeleton is thus of a distinctly higher type than in recent Cyclostomes, and lends support to the view that the latter are degenerate. There is a caudal fin supported by forked rays. The cranium consists of an anterior, probably trabecular, region (*t. p.*), and of a posterior region (*p. a.*) which seems to answer to the

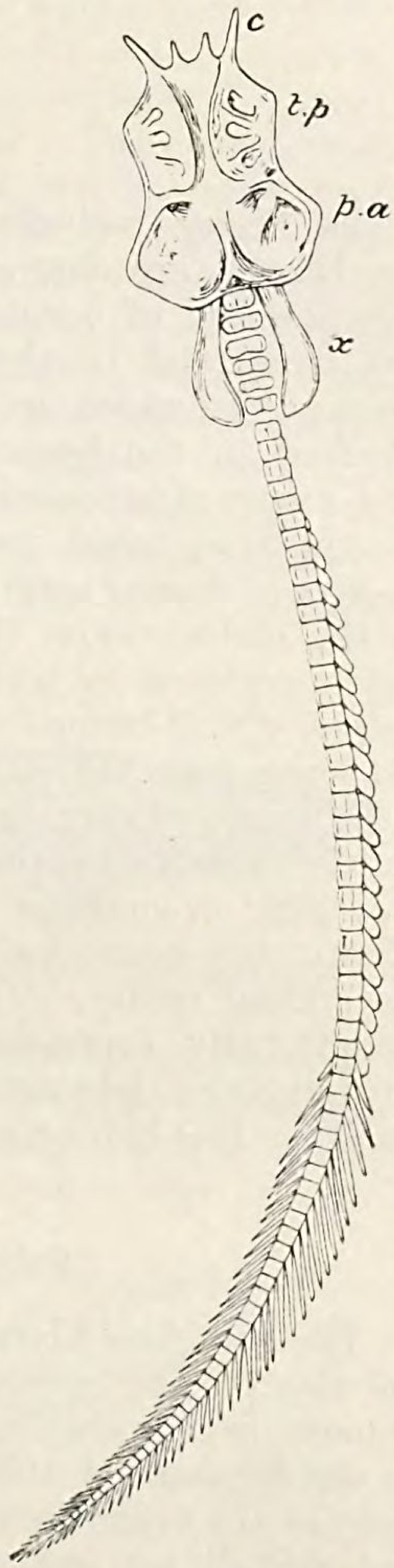


FIG. 765.—**Palæospondylus gunni** (magnified). *c*. cirri; *p.a*. parachordal and auditory region; *t.p*. trabecular region; *x*. backward processes of skull. (After Traquair.)

parachordals and auditory capsules. Just in advance of the anterior region is a ring-shaped opening surrounded by cirri (*c.*), and considered to be the nasal aperture. The posterior region gives off paired plates (*x.*) which may perhaps correspond with the dorsal longitudinal bars of the branchial basket in the Lamprey.

CLASS II.—PISCES.

The Pisces, including the cartilaginous and bony Fishes and the Dipnoi, are Craniata which have the organs both of respiration and of locomotion adapted for an aquatic mode of life. The chief, and in the majority the only, organs of respiration are the gills, which are in the form of series of vascular processes attached to the branchial arches and persisting throughout life. The organs of locomotion are the paired pectoral and pelvic fins, and the unpaired dorsal, ventral, and caudal; these are all supported by fin-rays of dermal origin. A dermal exoskeleton is usually present. In the endoskeleton the notochord is usually more or less completely replaced by vertebræ; there is a well-developed skull and a system of well-formed visceral arches, of which the first forms upper and lower jaws, the latter movably articulating with the skull, and both nearly always bearing teeth. There is frequently an air-bladder, which in certain exceptional cases acquires the function of a lung or chamber for breathing air. The hypophysis is not in any way connected with the nasal chambers, and lies within the cranial cavity. There is a pair of nasal chambers which only exceptionally communicate internally with the mouth-cavity. The auditory labyrinth contains the three typical semicircular canals. The kidney is a persistent mesonephros.

Sub-Class I.—Elasmobranchii.

The sub-class Elasmobranchii comprises the Sharks, Dog-fishes, and Rays. The skeleton of these fishes, like that of the Cyclostomata, is composed essentially of cartilage, and, though there may be ossifications in the substance of the cartilage, distinct bones, such as are found in all higher groups, with the exception of the Holocephali, are not present. The dermal fin-rays, supported on the cartilaginous skeleton of the fin, are of horn-like constitution. There is never (in recent forms) an operculum or gill-cover. There is a cloaca, the external opening of which serves as a common outlet for the rectum and the renal and reproductive ducts. Among some of the fossil representatives of this group are to be found the most primitive of all known Fishes.

1.—Example of the Sub-Class: The Dog-Fish (*Scyllium canicula* or *Chiloscyllium fuscum*).

General external features.—The general shape of the body (Fig. 766) may be roughly described as fusiform; at the anterior, or head, end it is broader and depressed; posteriorly it tapers gradually and is compressed from side to side. The head terminates anteriorly in a short blunt snout. The tail is narrow and bent upwards towards the extremity. The colour is grey with brown markings, or dark-brown above, lighter underneath. The entire surface is covered closely with very minute hard *placoid scales* or *dermal teeth* somewhat larger on the upper surface than on the lower. These are pointed, with the points directed somewhat backwards, so that the surface appears rougher when the hand is passed over it forwards than when it is passed in the opposite direction. When examined closely each scale is found to be a minute spine situated on a broader base. The spine consists

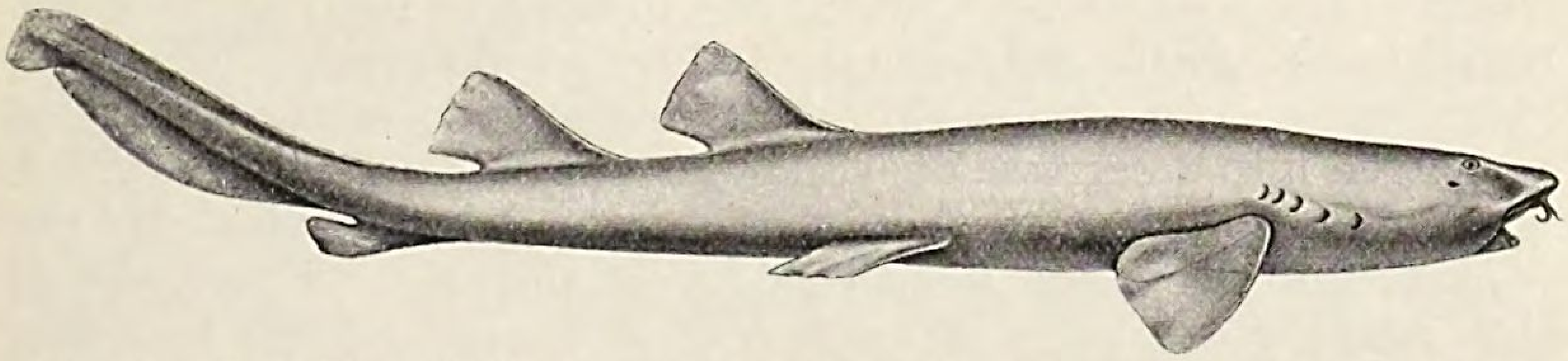


Fig. 766.—**Dog-Fish (Chiloscyllium modestum).** Lateral view. (After Günther.)

of dentine covered with a layer of enamel; the base is composed of bone, and the whole scale has thus the same essential structure as a tooth. Along each side of the head and body runs a faint depressed longitudinal line or slight narrow groove—the *lateral line.*

As in Fishes in general, two sets of fins are to be recognised—the *unpaired* or *median* fins, and the *paired* or *lateral.* These are all flap-like outgrowths, running vertically and longitudinally in the case of the median fins, nearly horizontally in the case of the lateral: they are flexible, but stiffish, particularly towards the base, owing to the presence of a supporting framework of cartilage. Of the median fins two—the *dorsal*—are situated, as the name indicates, on the dorsal surface: they are of triangular shape; the anterior, which is the larger, is situated at about the middle of the length of the body, the other a little further back. The *caudal* fringes the tail: it consists of a narrower dorsal portion and a broader ventral, continuous with one another round the extremity of the tail, the latter divided by a notch into a larger, anterior, and a smaller, posterior lobe. The tail is *heterocercal, i.e.*, the posterior extremity of the spinal column is bent upwards and lies in the dorsal portion of the caudal fin. The *ventral* or so-called *anal* fin is situated on

the ventral surface, opposite the interval between the anterior and posterior dorsals (in *Scyllium*); it resembles the latter in size and shape.

Of the *lateral fins* there are two pairs, the pectoral and the pelvic. The *pectoral* are situated at the sides of the body, just behind the head. The *pelvic*, which are the smaller, are placed on the ventral surface, close together, in front of the middle of the body. In the males the bases of the pelvic fins are united together in the middle line, and each has connected with it a *clasper* or *copulatory organ*. The latter is a stiff rod, on the inner and dorsal aspect of which is a groove leading forwards into a pouch-like depression in the base of the fin.

The *mouth*—a transverse, somewhat crescentic opening—is situated on the ventral surface of the head, near its anterior end. In front and behind it is bounded by the upper and lower jaws, each bearing several rows of teeth with sharp points directed backwards. The nostrils are situated one in front of each angle of the mouth, with which each is connected by a wide groove—the *naso-buccal groove*. In Chiloscyllium the outer edge of the groove is prolonged into a narrow subcylindrical appendage—the *barbel*. A small rounded aperture, the *spiracle*—placed just behind the eye—leads into the large mouth cavity, or pharynx. Five pairs of slits running vertically on each side of the neck—the *branchial slits*—also lead internally into the mouth cavity. A large median opening on the ventral surface at the root of the tail, between the pelvic fins, is the opening leading into the cloaca, or chamber forming the common outlet for the intestine and the renal and reproductive organs. A pair of small depressions, the *abdominal pores*, situated behind the cloacal opening, lead into narrow passages opening into the abdominal cavity.

The **skeleton** is composed entirely of cartilage, with, in certain places, depositions of calcareous salts. As in Vertebrates in general, we distinguish two sets of elements in the skeleton—the axial set and the appendicular, the former comprising the skull and spinal column, the latter the limbs and their arches.

The *spinal column* is distinguishable into two regions—the region of the trunk and the region of the tail. In the trunk region each vertebra (Fig. 767, *A*) consists of a centrum (*cent.*), neural arch (*neur.*), and transverse processes (*tr.*). In the caudal region there are no transverse processes, but *inferior* or *hæmal arches* (B, *haem.*) take their place. The centra of all the vertebræ are deeply biconcave or *amphicœlous*, having deep conical concavities on their anterior and posterior surfaces. Through the series of centra runs the notochord, greatly constricted in the centrum itself, dilated in the large spaces formed by the apposition of the amphicœlous centra of adjoining vertebræ, where it forms a pulpy mass. The concave anterior and posterior surfaces of the centra are covered by a dense

calcified layer, and eight radiating lamellæ of bone (*C*) run longitudinally through the substance of the centrum itself. The centra, unlike those of the higher forms, are developed as chondrifications of the sheath of the notochord into which cells of the skeletogenous layer have migrated (p. 66). Each neural arch consists of a pair of rod-like *neural processes*, which form the sides, and two pairs of compressed *neural plates* (one placed opposite the centrum, the other or *intercalary cartilage*, opposite the interval between adjoining centra) (Fig. 768), which form the roof of the arch, together with usually two nodules—the representatives of *neural spines* (*sp.*)—which form the keystones. The transverse processes are very short: connected with each of them is a cartilaginous rudimentary *rib* (*r.*) about half an inch in length.

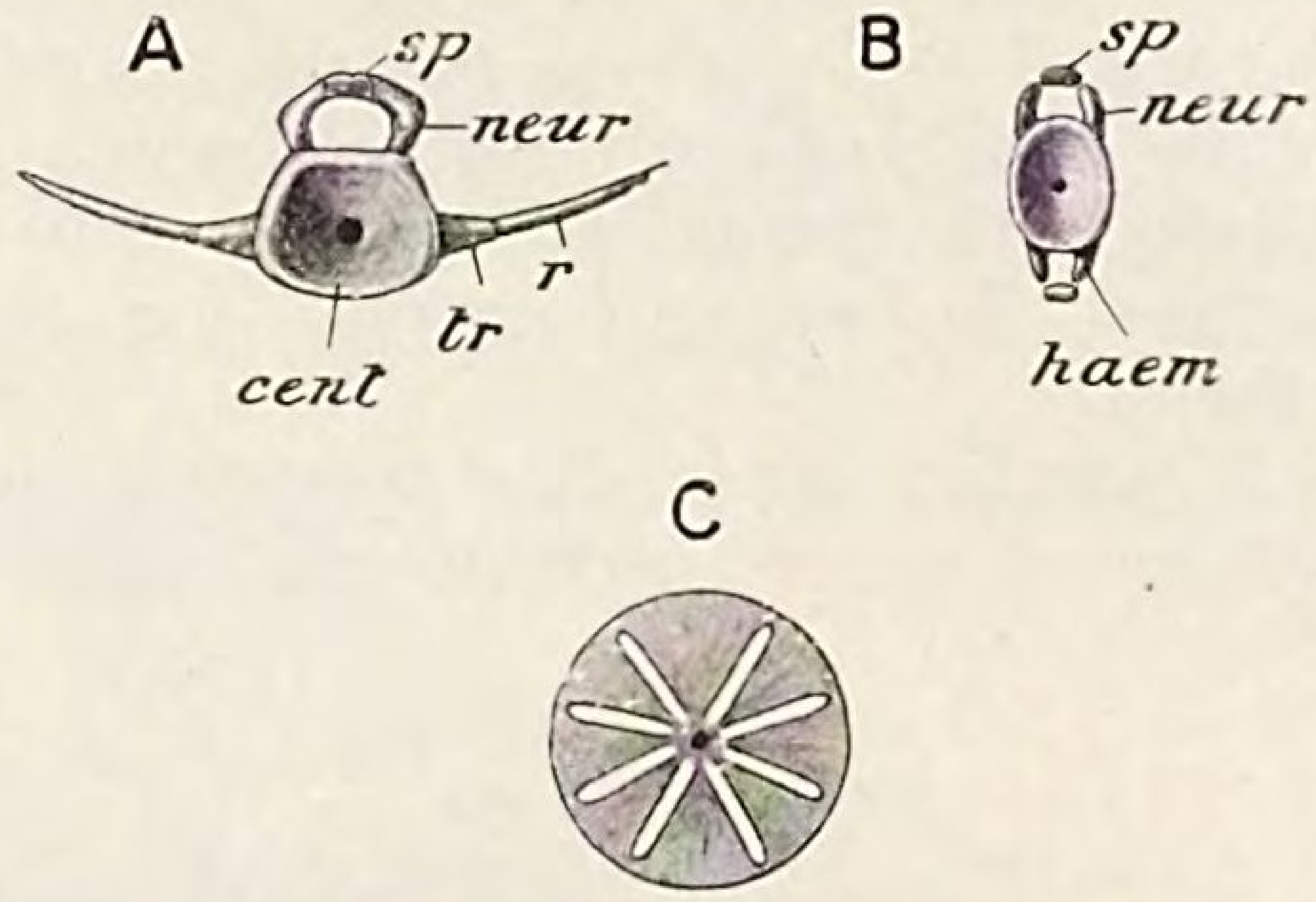


FIG. 767.—**Chiloscyllium,** vertebræ. *A*, end view of trunk vertebra. *cent.* centrum; *neur.* neural plate and process; *sp.* neural spines; *r.* ribs; *tr. proc.* transverse processes. *B*, lateral view of the same. *hæm.* hæmal arch; *neur.* neural arch. *C*, transverse section of a centrum, showing radiating lamellæ of bone.

The *cranium* (Fig. 768) is a cartilaginous case, the wall of which is continuous throughout, and not composed, like the skulls of higher Vertebrates, of a number of distinct elements (bones) fitting in together. At the anterior end is a *rostrum*, consisting in Scyllium of three cartilaginous rods converging as they extend forwards and meeting at their anterior ends. At the sides of the base of this are the *olfactory capsules* (*olf.*)—thin rounded cartilaginous sacs opening widely below—the cavities of the two capsules being separated from one another by a thin septum. The part of the roof of the cranial cavity behind and between the olfactory capsules is formed, not of cartilage, but of a tough fibrous membrane, and the space thus filled in is termed the *anterior fontanelle*: in contact with the lower surface of the membrane is the pineal body, to be afterwards mentioned in the account of the brain. Each side-wall of this part of the skull presents a deep concavity—the *orbit*—over which is a ridge-like prominence, the *supra-orbital crest*, terminating anteriorly and posteriorly in obscure processes termed respectively the *præ-orbital* and *post-orbital processes*. Below the orbit is a longitudinal *infra-orbital* ridge.

Behind the orbit is the *auditory region* of the skull—a mass of cartilage in which the parts of the membranous labyrinth of the internal ear are embedded. On the upper surface of this posterior

portion of the skull are two small apertures situated n a mesial depression. These are the openings of the *aqueductûs vestibuli* (*endolymphatic ducts*), leading into the vestibule of the membranous labyrinth. Behind this again is the *occipital region*, forming the posterior boundary of the cranial cavity, and having in the middle a large rounded aperture—the *foramen magnum*—through which the spinal cord contained in the neural canal and protected by the neural arches of the vertebræ, becomes continuous with the brain, lodged in the cranial cavity. On either side of this is an articular surface—the *occipital condyle*—for articulation with the spinal column.

A number of smaller apertures, or *foramina*, chiefly for the passage of nerves, perforate the wall of the skull. Behind and to

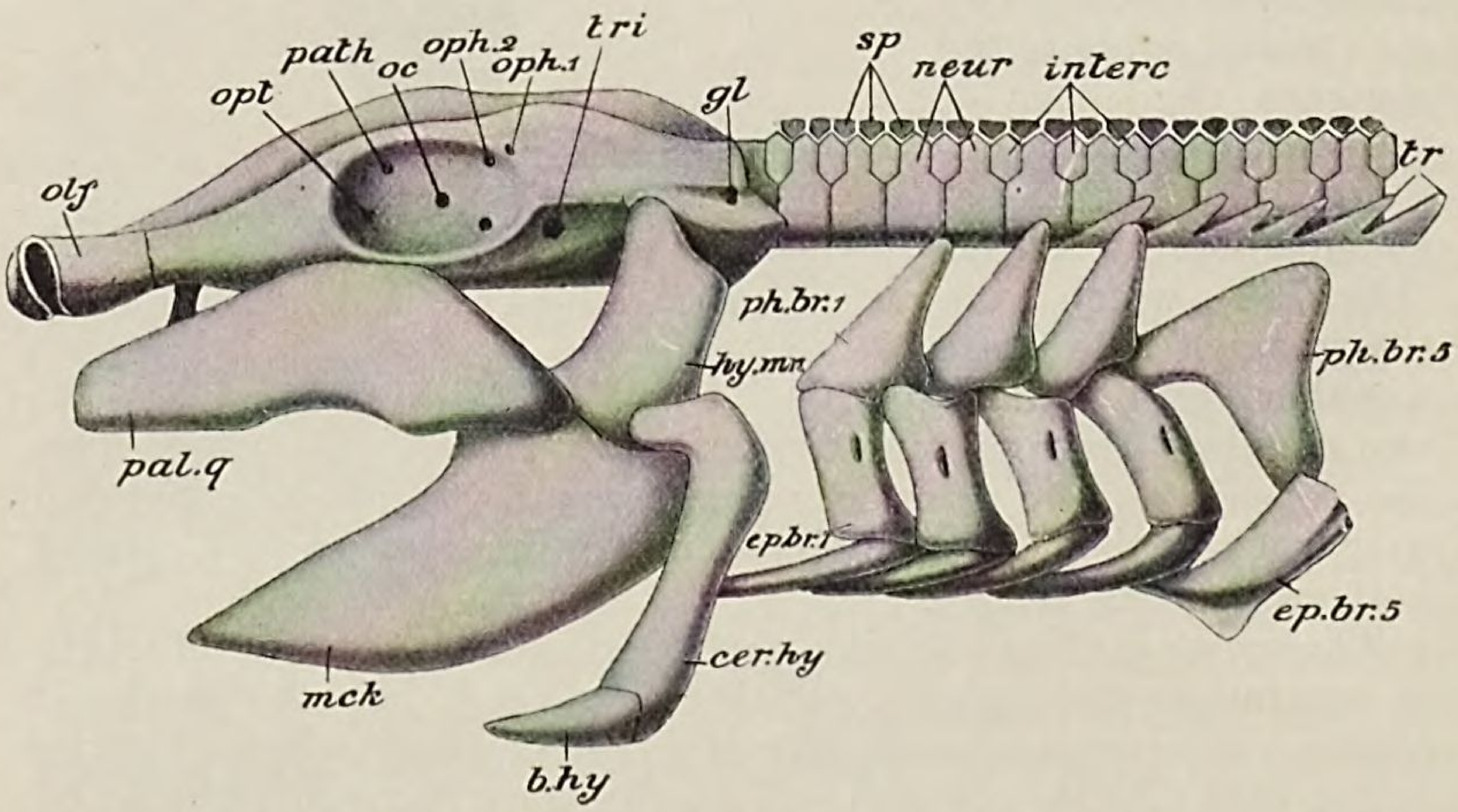


Fig. 768.—**Chiloscyllium,** lateral view of skull with visceral arches and anterior part of spinal column; the branchial rays are not represented. The skull and hyoid arch are somewhat drawn downwards, so that the hyoid and first branchial arch are not exactly in their natural relations. *br.*1—*br.*5 branchial arches; *cer. hy.* cerato-hyal; *ep. br.* epibranchials; *gl.* aperture for glosso-pharyngeal nerve; *b. hy.* basi-hyal; *hy. mn.* hyo-mandibular; *interc.* intercalary plates; *Mck.* Meckel's cartilage; *neur.* neural processes; *olf.* olfactory capsule; *oc.* foramen for oculo-motor; *opt.* optic foramen; *pal. q.* palato-quadrate; *path.* foramen for 4th nerve; *ph. br.*1 first pharyngo-branchial; *ph. br.*5 fifth pharyngo-branchial; *sp.* neural spines; *tr.* transverse processes and ribs; *tri.* foramen for trigeminal nerve.

the outer side of the anterior fontanelle is the aperture for the ophthalmic branch of the fifth, or trigeminal, nerve. Piercing the inner wall of the orbit are foramina through which the optic nerves, or second pair of cranial nerves (*opt.*); the oculo-motor (*oc.*), or third; the pathetic, or fourth (*path.*); the trigeminal, or fifth; the abducent, or sixth; and the facial, or seventh, gain an exit from the interior of the cranial cavity. Just behind the auditory region is the foramen for the glosso-pharyngeal, and in the posterior wall of the skull, near the foramen magnum, is the foramen for the vagus.

In close connection with the cranium are a number of cartilages

composing the *visceral arches* (Figs. 768 and 769). These are incomplete hoops of cartilage, mostly segmented, which lie in the sides and floor of the mouth-cavity or pharynx. The first of these forms the upper and lower jaws. The upper jaw, or *palato-quadrate* (*pal. q.*), consists of two stout rods of cartilage firmly bound together in the middle line and bearing the upper (or anterior) series of teeth. The lower jaw, or *Meckel's cartilage* (*Mck.*), likewise consists of two stout cartilaginous rods firmly united together in the middle line, the union being termed the *symphysis*. At their outer

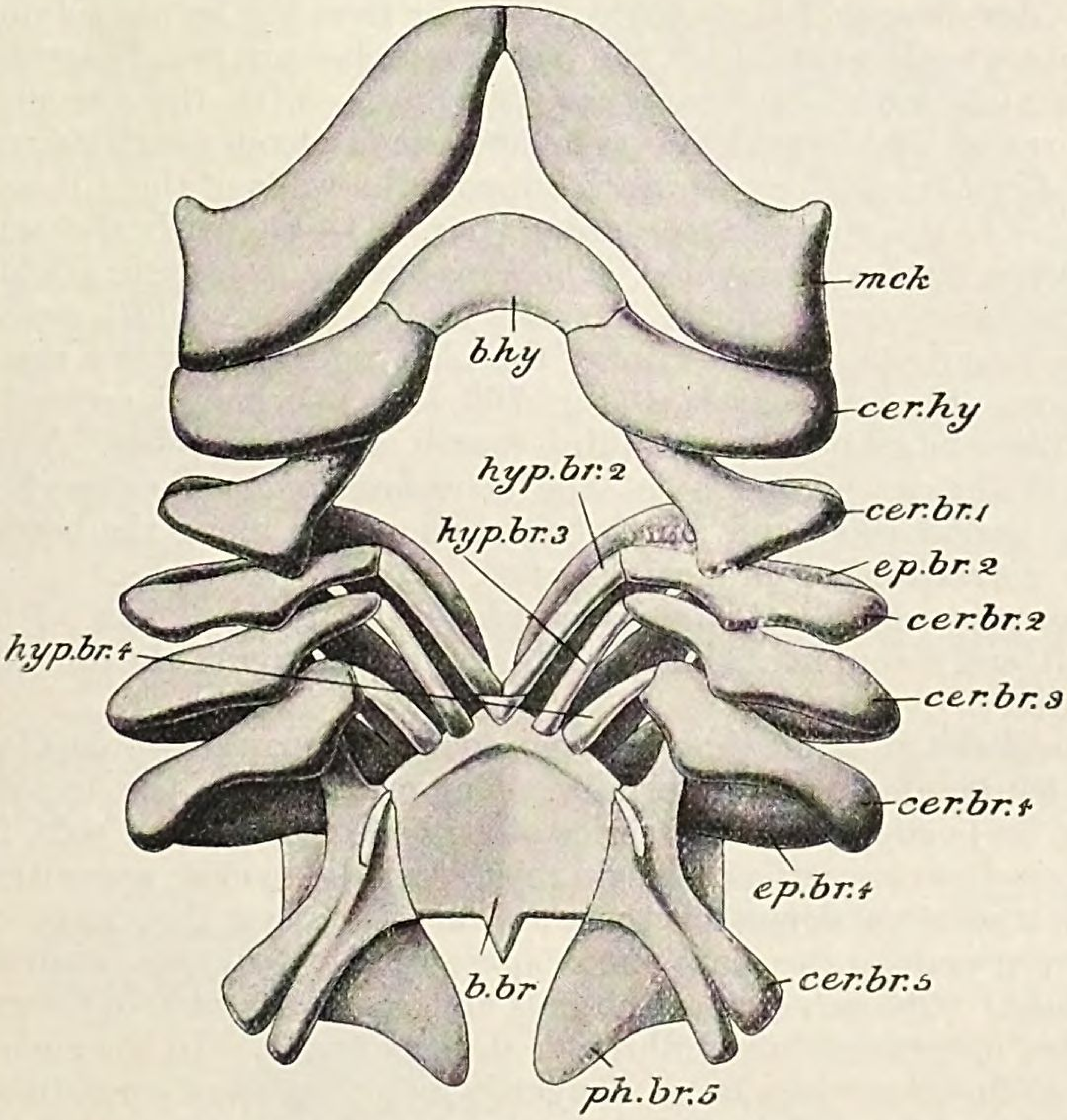


FIG. 769.—**Chiloscyllium,** ventral view of the visceral arches. Letters as in preceding figure. In addition, *b. br.* basi-branchial plate ; *cer. br.* cerato-branchials ; *hyp. br.* hypo-branchials.

ends the upper and lower jaws articulate with one another by a movable joint. In front the upper jaw is connected by a ligament with the base of the skull.

Immediately behind the lower jaw is the *hyoid arch*. This consists of two cartilages on each side, and a mesial one in the middle below. The uppermost cartilage is the *hyo-mandibular* (*hy. mn.*): this articulates by its proximal end with a distinct articular facet on the auditory region of the skull; distally it is connected by ligamentous fibres with the outer ends of the palato-quadrate

and Meckel's cartilage. The lower lateral cartilage is the *cerato-hyal* (*cer. hy.*). Both the hyo-mandibular and cerato-hyal bear a number of slender cartilaginous rods—the branchial rays of the hyoid arch. The mesial element, or *basi-hyal* (*b. hy.*), lies in the floor of the pharynx. Behind the hyoid arch follow the *branchial arches*, which are five in number. Each branchial arch, with exceptions to be presently noted, consists of four cartilages. The uppermost of these—*pharyngo-branchial* (*ph. br.*^{1}–*ph. br.*^{5})—lie in the dorsal wall of the pharynx, not far from the spinal column; the pharyngo-branchials of the last two arches are fused together. The next in order—the *epibranchials* (*ep. br.*)—with the exception of those of the last arch, bear a number of slender cartilaginous rods—the *branchial rays*—which support the walls of the gill-sacs; and the next—the *cerato-branchials* (*cer. br.*)—are, with the same exception, similarly provided. The *hypo-branchials* (*hyp. br.*), which succeed these, are absent in the case of the first and fifth arches. In the middle line on the floor of the pharyngeal cavity is a mesial cartilage—the *basi-branchial* (Fig. 769, *b. br.*)—which is connected with the ventral ends of the third, fourth, and fifth arches. Three pairs of slender curved rods—the *extra-branchials*—lie superficial to the second, third, and fourth branchial arches, along the borders of the corresponding branchial clefts.

Two pairs of delicate *labial* cartilages lie at the sides of the mouth, and a couple at the margins of the openings of the olfactory capsules.

The skeleton of all the fins—paired and unpaired—presents a considerable degree of uniformity. The main part of the expanse of the fin is supported by a series of flattened segmented rods, the *pterygiophores* or cartilaginous fin rays, which lie in close apposition: in the case of the dorsal fins these are calcified along their axes. At the outer ends of these are one or more rows of polygonal plates of cartilage. On each side of the rays and polygonal cartilages are a number of slender horny fibres of dermal origin. In the smaller median fins there may be an elongated rod of cartilage constituting the skeleton, or cartilage may be entirely absent. In the pectoral fin (Fig. 770) the fin rays are supported on three *basal cartilages* articulating with the *pectoral arch*. The latter (*pect.*) is a strong hoop of cartilage incomplete dorsally, situated immediately behind the last of the branchial arches. It consists of a dorsal, or *scapular*, and a ventral, or *coracoid* portion, the coracoid portions of opposite sides being completely continuous across the middle line, while the scapular are separated by a wide gap in which the spinal column lies. Between the two portions are the three articular surfaces for the three basal cartilages. The coracoid portions are produced forwards in the middle line into a flattened process supporting the floor of the pericardial cavity in which the heart is lodged. The three basal cartilages of the fin are named,

respectively, the anterior, *pro-pterygium* (*pro.*), the middle, *meso-pterygium* (*meso.*), and the posterior, *metapterygium* (*meta.*). Of these the first is the smallest, and the last the largest: the first bears only one large ray; the other two bear twelve or more, differently arranged in the two genera.

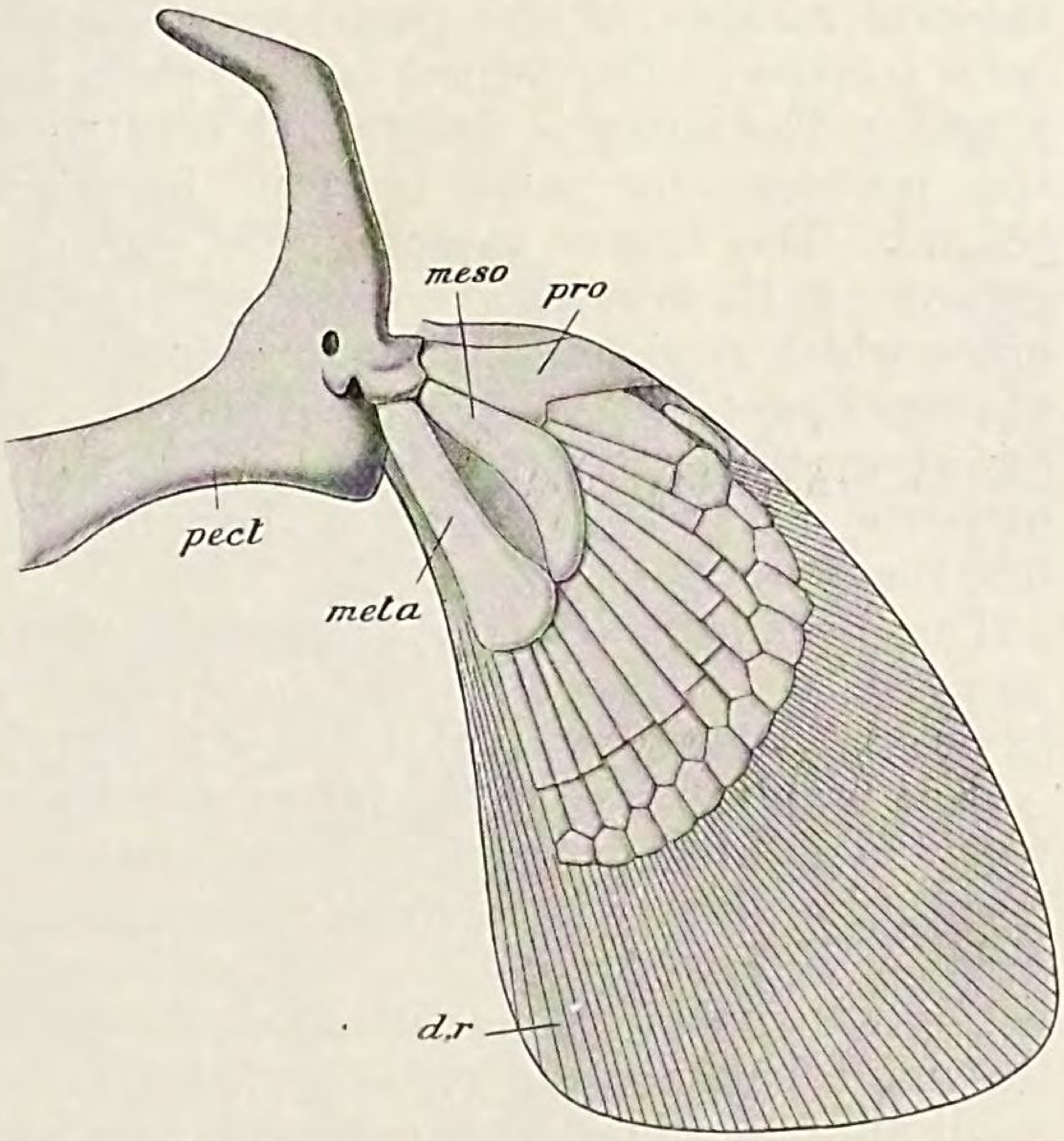


FIG. 770.—**Chiloscyllium,** pectoral arch and fin. *d. r.* dermal horny rays; *meso.* mesopterygium; *meta.* metapterygium; *pect.* pectoral arch; *pro.* propterygium.

The *pelvic fin* (Fig. 771) has only a single basal cartilage (*meta.*) articulating with the *pelvic arch*, with which also one or two of the fin rays articulate directly. The pelvic arch (*pelv.*) is a nearly straight bar of cartilage which runs transversely across the ventral surface of the body, just in front of the cloacal opening.

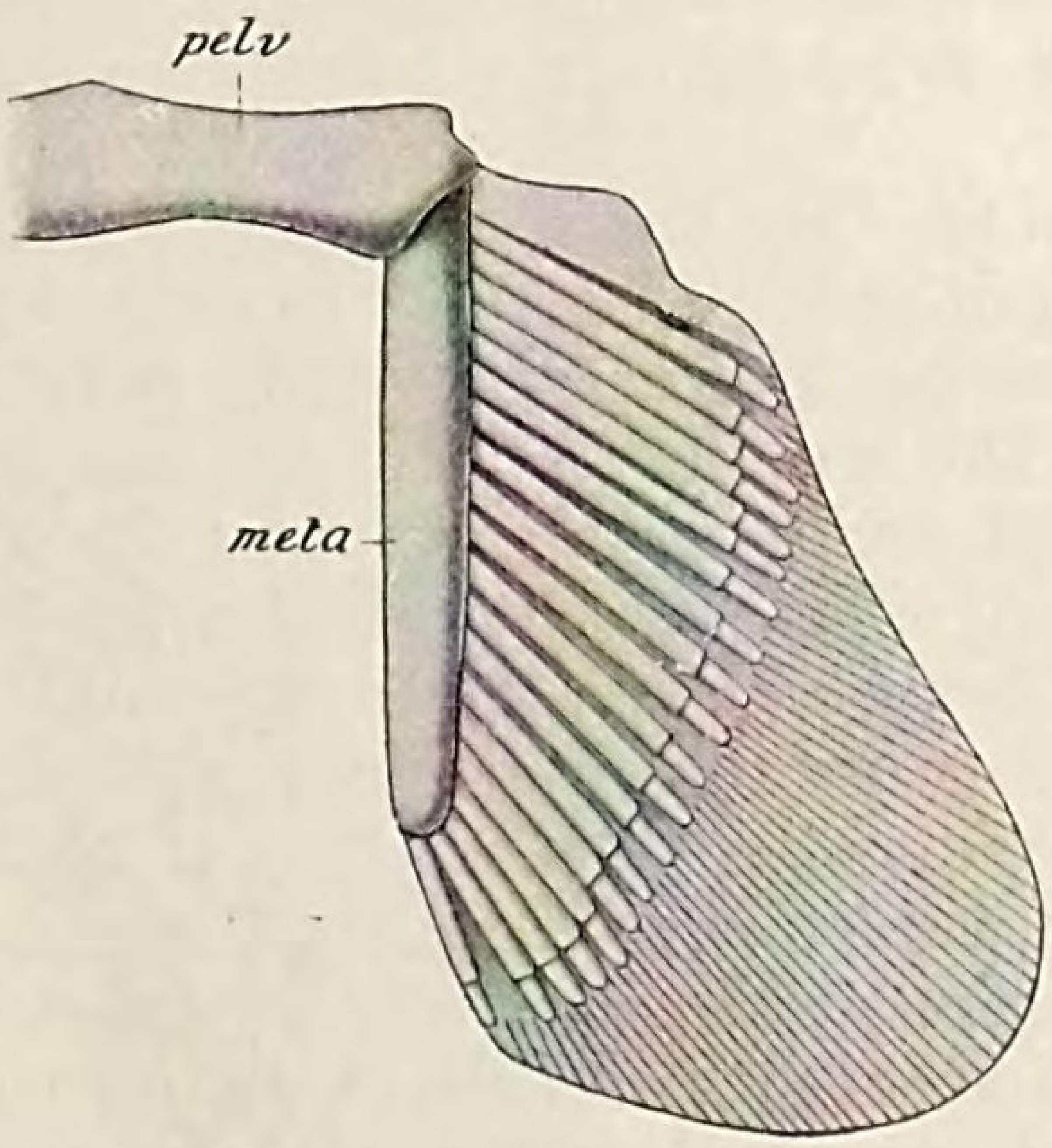


FIG. 771.—**Chiloscyllium,** pelvic arch and pelvic fin. *meta.* metapterygium; *pelv.* pelvic arch.

Enteric canal (Fig. 772).—The mouth leads into a very wide cavity, the *pharynx*, into which open at the sides the internal apertures of the branchial clefts and of the spiracle. From this runs backwards a short wide tube—the *œsophagus* (*œs.*)—which passes behind into the stomach. The stomach is a U-shaped organ, with a long left limb continuous with the œsophagus, and a short right passing into the intestine. At the *pylorus* (*pyl.*)—the point where the stomach passes into the intestine—is a slight constriction, followed by a thickening. The

intestine consists of two parts—*small intestine* or *duodenum*, and *large intestine.* The former is very short, only an inch or two in length. The latter is longer and very wide; it is divisible into two portions—the *colon* (*col.*) in front and the *rectum* (*rect.*) behind. The former is very wide and is characterised by the presence in its interior of a *spiral valve*, a fold of the mucous membrane which runs spirally round its interior, and both retards the too rapid passage of the food and affords a more extensive surface for absorption. The rectum differs from the colon in being narrower and in the absence of the spiral valve; it opens behind into the cloaca.

There is a large *liver* (*liv.*) consisting of two elongated lobes. A rounded sac—the *gall-bladder* (*g. bl.*)—lies embedded in the left lobe at its anterior end. The duct of the liver—the *bile-duct* (*b. dct.*)—runs from the liver to the intestine. Proximally it is connected with the gall-bladder, and by branch-ducts with the right and left lobes of the liver. It opens into the commencement of the colon.

The *pancreas* (*pancr.*) is a light-coloured compressed gland consisting of two main lobes with a broad connecting isthmus, lying in the angle between the right-hand limb of the stomach and the small intestine. Its duct enters the wall of the small intestine and runs in it for about half an inch, opening eventually at the point where the small intestine passes into the colon.

Connected with the rectum on its dorsal aspect is an oval gland—the *rectal gland* (*rect. gl.*)—about three-quarters of an inch in length.

The *spleen* (*spl.*) is a dark-red or purple body attached to the convexity of the U-shaped stomach and sending a narrow lobe along the right-hand limb.

The **organs of respiration** in the Dog-fish are the *gills*, situated in the five *gill-pouches.* Each gill-pouch (Fig. 773) is an antero-posteriorly compressed cavity opening internally into the pharynx and externally by the gill-slit. The walls of the pouches are supported by the branchial and hyoid arches with their rays, the first pouch being situated between the hyoid and first branchial arches, the last between the fourth and fifth branchial arches. On the anterior and posterior walls of the pouches are the *gills*, each hemibranch consisting of a series of close-set parallel folds or plaits of highly vascular mucous membrane. Separating adjoining gill-pouches, and supporting the gills, are a series of broad *interbranchial septa*, each containing the corresponding branchial arch with its connected branchial rays. The most anterior hemibranch is borne on the posterior surface of the hyoid arch. The last gill-pouch differs from the rest in having gill-plaits on its anterior wall only. On the anterior wall of the spiracle is a rudimentary gill—the *pseudo-branch* or *spiracular gill*—in the form of a few slight ridges.

Blood system.—The *heart* is situated in the pericardial cavity,

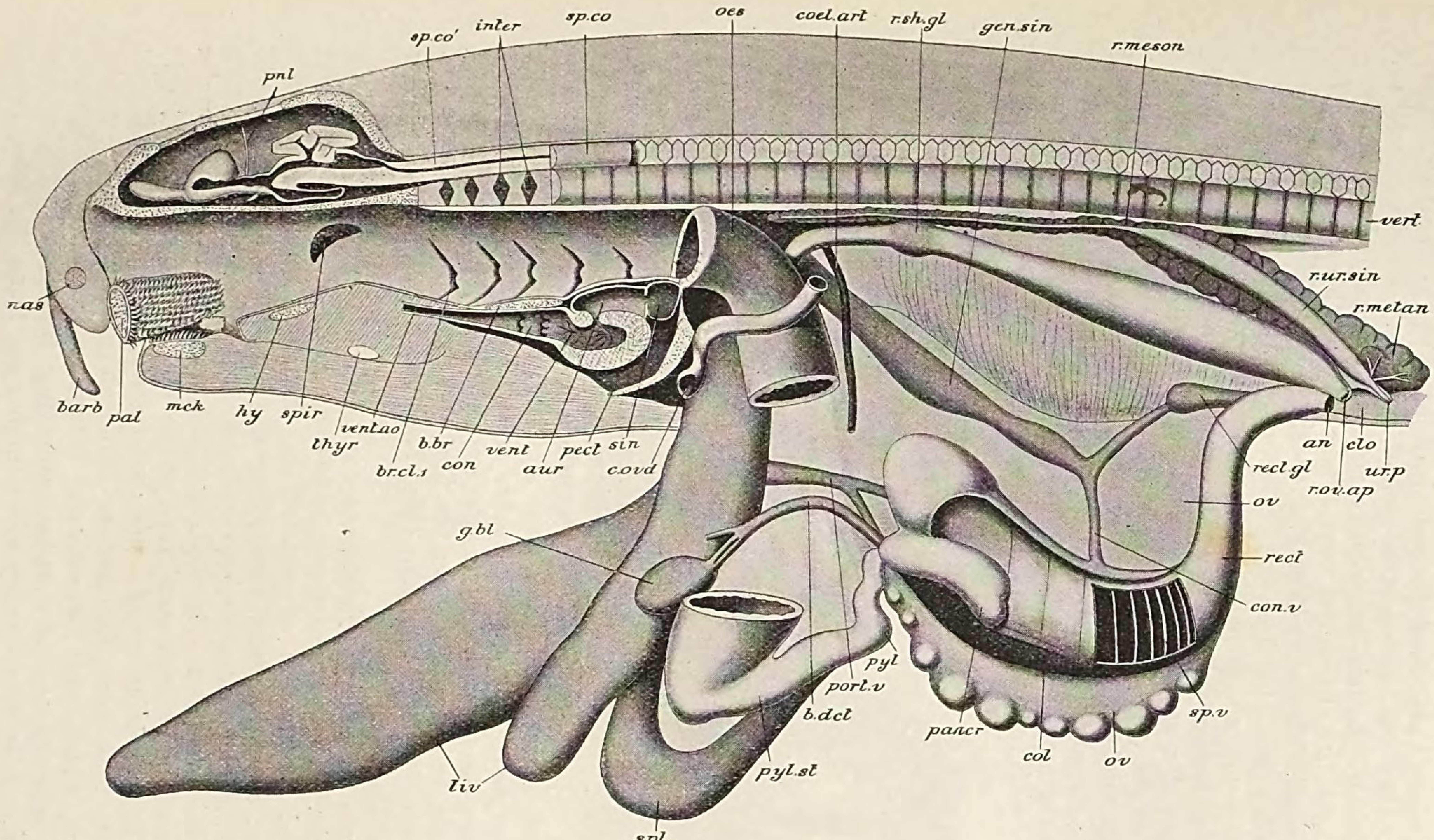


FIG. 772.—**Chiloscyllium,** lateral dissection. The left-hand side of the body-wall has been removed so as to bring into view the various parts of the digestive, renal, and reproductive systems. The left oviduct and kidney have been removed; the cloaca has been opened. The head is represented in median vertical section. The chambers of the heart have been opened. *an.* opening of rectum into cloaca; *aur.* auricle; *barb.* barbule; *b. br.* basi-branchial plate; *b. dct.* bile-duct; *br. cl.* internal branchial clefts; *clo.* cloaca; *cœl.* cœliac artery (cut short); *col.* colon; *con.* conus; *con. v.* connecting vein between the genital (ovarian) sinus and the hepatic portal system; *c. ovd.* common oviduct; *g. bl.* gall-bladder; *gen. sin.* genital sinus; *hy.* basi-branchial; *liv.* liver; *Mck.* Meckel's cartilage; *nas.* nasal cartilage; *œs.* œsophagus; *ov.* ovary; *ovd.* oviduct; *pal.* palato-quadrate; *pancr.* pancreas; *pect.* pectoral arch; *pnl.* stalk of pineal body; *pyl.* pylorus; *pyl. st.* pyloric portion of stomach; *rect.* rectum; *rect. gl.* rectal gland; *r. meson.* right kidney; *r. metan.* posterior portion of kidney; *r. ov. ap.* right ovarian aperture; *r. sh. gl.* right shell-gland; *r. ur. sin.* right urinary sinus; *sin. ven.* sinus venosus; *sp. co.* spinal cord; *sp. co'.* anterior part of spinal cord in median vertical section; *spir.* spiracle; *spl.* spleen; *sp. v.* spiral valve; *thyr.* thyroid; *ur. p.* urinary papilla; *vent. ao.* ventral aorta; *vert.* centra of vertebræ.

on the ventral aspect of the body, in front of the pectoral arch, and between the two series of branchial pouches. Its dorsal wall is supported by the basi-branchial cartilage. Placing it in communication with the abdominal cavity is a canal—the *pericardio-peritoneal canal.* The heart (Fig. 772) consists of four chambers—*sinus venosus* (*sin. ven.*), *auricle* (*aur.*), *ventricle* (*vent.*), and *conus arteriosus* (*con.*), through which the blood passes in the order given. The *sinus venosus* is a thin-walled, transverse, tubular chamber, into the ends of which the great veins open. It opens into the auricle by an aperture, the *sinu-auricular* aperture. The *auricle* is a large, triangular, thin-walled chamber, situated in front of the sinus venosus and dorsal to the ventricle. Its apex is directed forwards, and its lateral angles project at the sides of the ventricle: it communicates with the ventricle by a slit-like aperture guarded by a two-lipped valve. The *ventricle* is a thick-walled, globular chamber, forming the most conspicuous part of the heart when looked at from the ventral surface. From it the *conus arteriosus* runs forwards as a median stout tube to the anterior end of the pericardial cavity, where it gives off the *ventral aorta.* It contains two transverse rows of valves, anterior and posterior, the former consisting of three, the latter of three or four. The *ventral aorta* (Fig. 774) gives origin to a series of paired *afferent branchial arteries* (*br. v.*), one for each branchial pouch. In Scyllium the two most posterior arise close together near the beginning of the ventral aorta, the third pair a little further forwards. The ventral aorta then runs forwards a little distance and bifurcates to form the two *innominate* arteries, right and left, each of which in turn bifurcates to form the first and second afferent vessels of its side. In Chiloscyllium (Fig. 774) the arrangement is somewhat different.

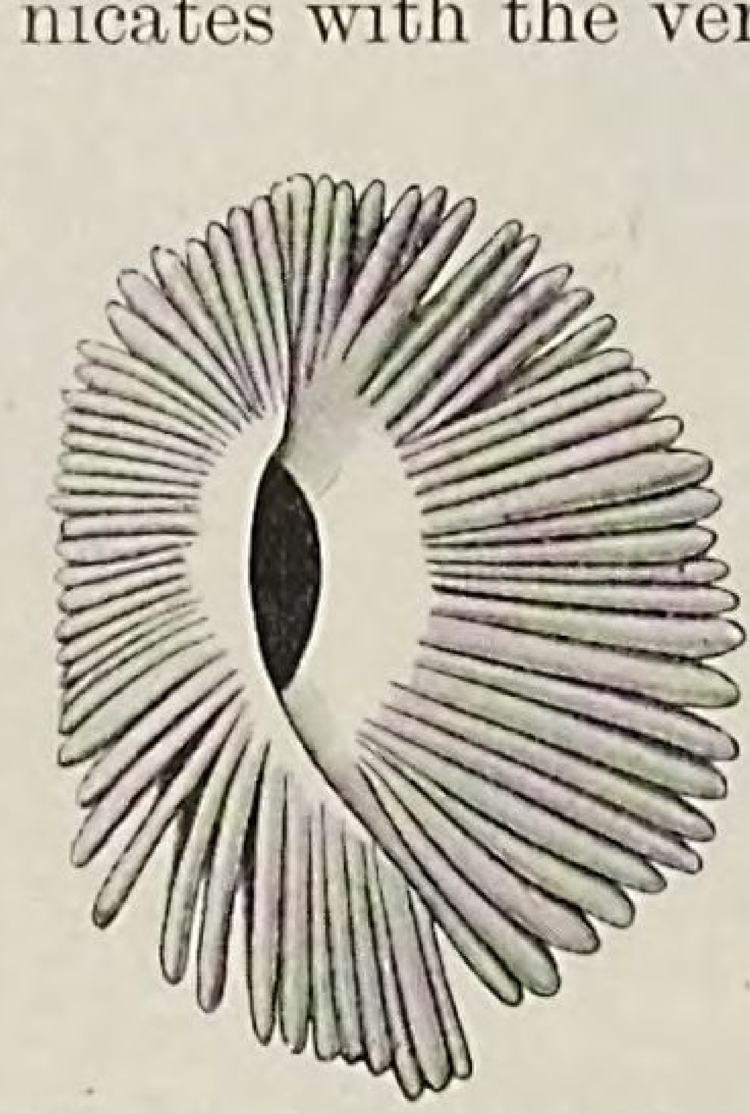


FIG. 773.—**Chiloscyllium.** Branchial sac exposed from the outside.

From the gills the blood passes by means of the *efferent branchial arteries.* These efferent vessels form a series of loops, one running around the margin of each of the first four internal branchial clefts: a single vessel runs along the anterior border of the fifth branchial cleft and opens into the fourth loop. The four main efferent branchial vessels run inwards and backwards from the loops under cover of the mucous membrane of the roof of the mouth to unite in a large median trunk—the *dorsal aorta.* From the first efferent vessel, that from the first or hyoidean gill, arises the *carotid artery,* which runs forwards and bifurcates to form the *internal* and *external carotid arteries,* supplying the head with arterial blood. A *hyoidean artery* arises further out from the same vessel,

and, after giving off branches to the pseudobranch, passes into the cranial cavity and joins the internal carotid of the opposite side.

The *dorsal aorta* runs backwards throughout the length of the body cavity, giving off numerous branches, and is continued as the *caudal artery*, which runs in the canal enclosed by the inferior arches of the caudal vertebræ. The first pair of branches are the *subclavian*, for the supply of the pectoral fins; these are given off between the third and fourth pairs of efferent arteries. The next large branch is the unpaired *cœliac* (Fig. 772, *cœl.*); this runs in the mesentery and divides into branches for the supply of the stomach and liver, the first part of the intestine, and the pancreas. The *anterior mesenteric* artery, also median, supplies the rest of the intestine and gives off branches to the reproductive organs. The *lienogastric* supplies part of the stomach, the spleen, and part of the pancreas. The *posterior mesenteric* is a small vessel mainly supplying the rectal gland. A pair of small *renal* arteries carry a small quantity of arterial blood to the kidneys, and a pair of *iliac* arteries, likewise of small size, supply the pelvic fins. In addition to

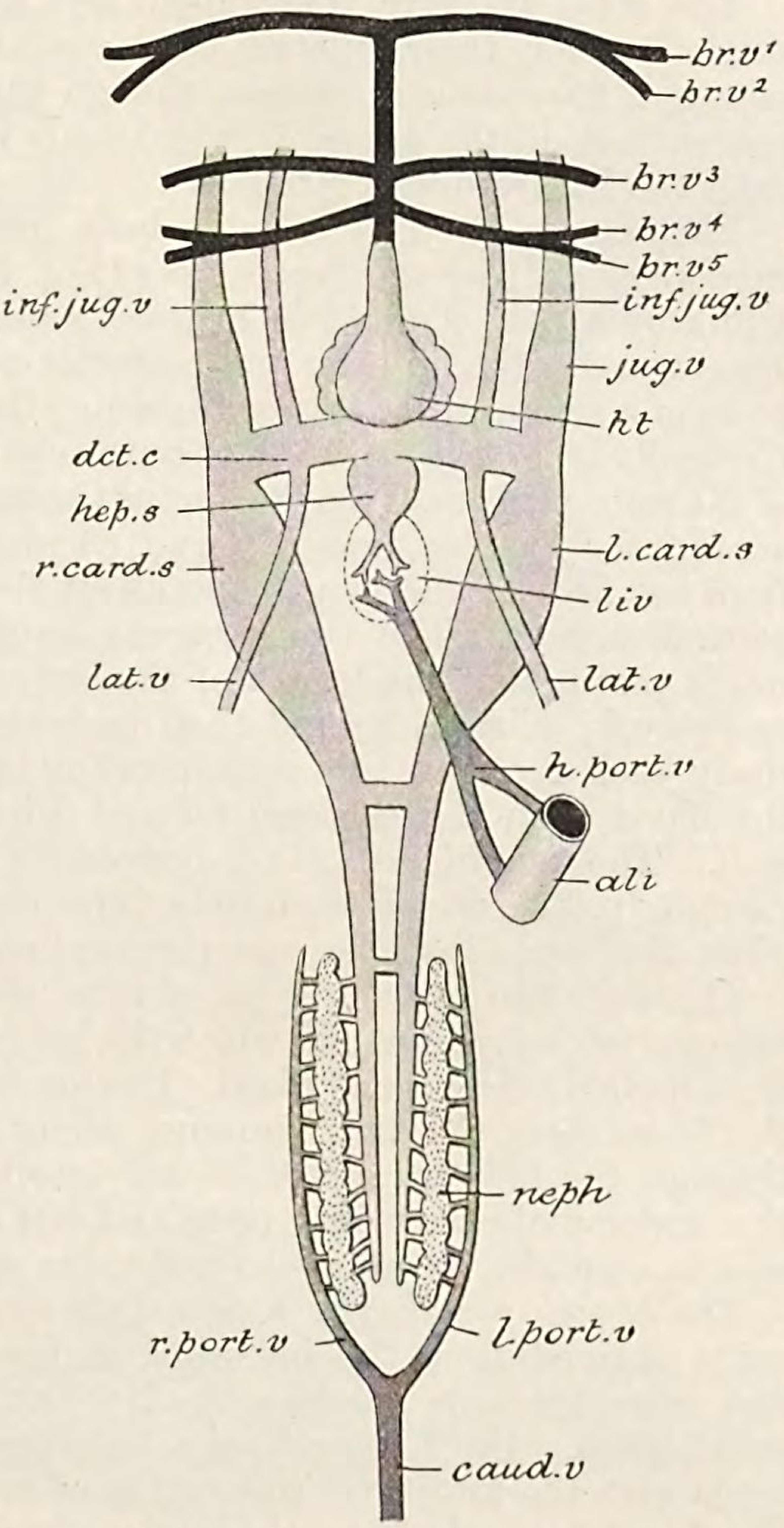


FIG. 774.—**Chiloscyllium.** Diagrammatic representation of the ventral aorta and afferent branchial arteries, and of the chief veins. *ali.* alimentary canal; *br. v.*¹-*br. v.*⁵ afferent branchial arteries; *caud. v.* caudal vein; *dct. c.* ductus Cuvieri; *ht.* heart; *hep. port. v.* hepatic portal vein; *hep. s.* hepatic sinus; *inf. jug. v.* inferior jugular vein or sinus; *jug.* jugular vein or sinus; *lat. v.* lateral vein; *liv.* liver; *l. card. s.* left cardinal sinus; *l. port. v.* left renal portal vein; *neph.* kidney; *r. card. s.* right posterior cardinal sinus; *r. port. v.* right renal portal vein.

these a number of small arteries, the *parietal*, supplying the wall of the body, are given off throughout the length of the aorta.

The *veins* are very thin-walled, and the larger trunks are remarkable for their dilated character, from which they have obtained the name of *sinuses*, though they are true vessels and not sinuses in the sense in which the word is used in dealing with the Invertebrates (*cf.* p. 87).

The venous blood is brought back from the head by a pair of *jugular* or *anterior cardinal sinuses* (Fig. 774, *jug. v.*), and from the trunk by a pair of *posterior cardinal sinuses.* At the level of the sinus venosus the anterior and posterior cardinals of each side unite to form a short, nearly transverse sinus, the *precaval sinus* or *ductus Cuvieri* (Fig. 774, *dct. c.*), which is continued into the lateral extremity of the sinus venosus. Into the ductus Cuvieri, about its middle, opens an *inferior jugular sinus* (*inf. jug. v.*) which brings back the blood from the floor of the mouth and about the branchial region of the ventral surface. The two posterior cardinal sinuses extend backwards throughout the length of the body cavity; in front they are enormously dilated, behind they lie between the kidneys. Anteriorly each receives the corresponding *subclavian vein*, bringing the blood from the pectoral fin and adjacent parts of the body-wall. The *lateral vein* (*l.v.*), instead of joining with the subclavian (p. 87), opens separately into the precaval. The *genital sinus* discharges into the posterior cardinal sinus.

There are two *portal* systems of veins, the *renal portal* and the *hepatic portal* (*hep. port. v.*), by which the kidneys and liver, respectively, are supplied with venous blood. The *caudal vein*, which brings back the blood from the tail, running, along with the caudal artery, through the inferior arches of the vertebræ, divides on entering the abdominal cavity into right and left *renal portal* veins, which end in a number of afferent renal veins supplying the kidneys.

The *hepatic portal* vein (*h. port. v.*) is formed by the confluence of veins derived from the intestine, stomach, pancreas, and spleen, and runs forwards to enter the liver a little to the right of the middle line. In Chiloscyllium a large branch connects the genital sinus with the intestinal tributaries of the hepatic portal system. The blood from the liver enters the sinus venosus by two *hepatic sinuses* placed close together.

Nervous System.—The fore-brain consists of a rounded, smooth prosencephalon (Fig. 775, V.H.), divided into two lateral parts by a very shallow median longitudinal groove. From its antero-lateral region each half gives off a thick cord, which dilates into a large mass of nerve-matter, the *olfactory lobe* (*L.ol.*), closely applied to the posterior surface of the corresponding olfactory capsule. The diencephalon (*ZH*) is comparatively small; its roof is very thin, while the floor is composed of two thickish masses

—the *optic thalami.* Attached to the roof is a slender tube, the *epiphysis cerebri* or *pineal body* (*Gp.*), which runs forwards and

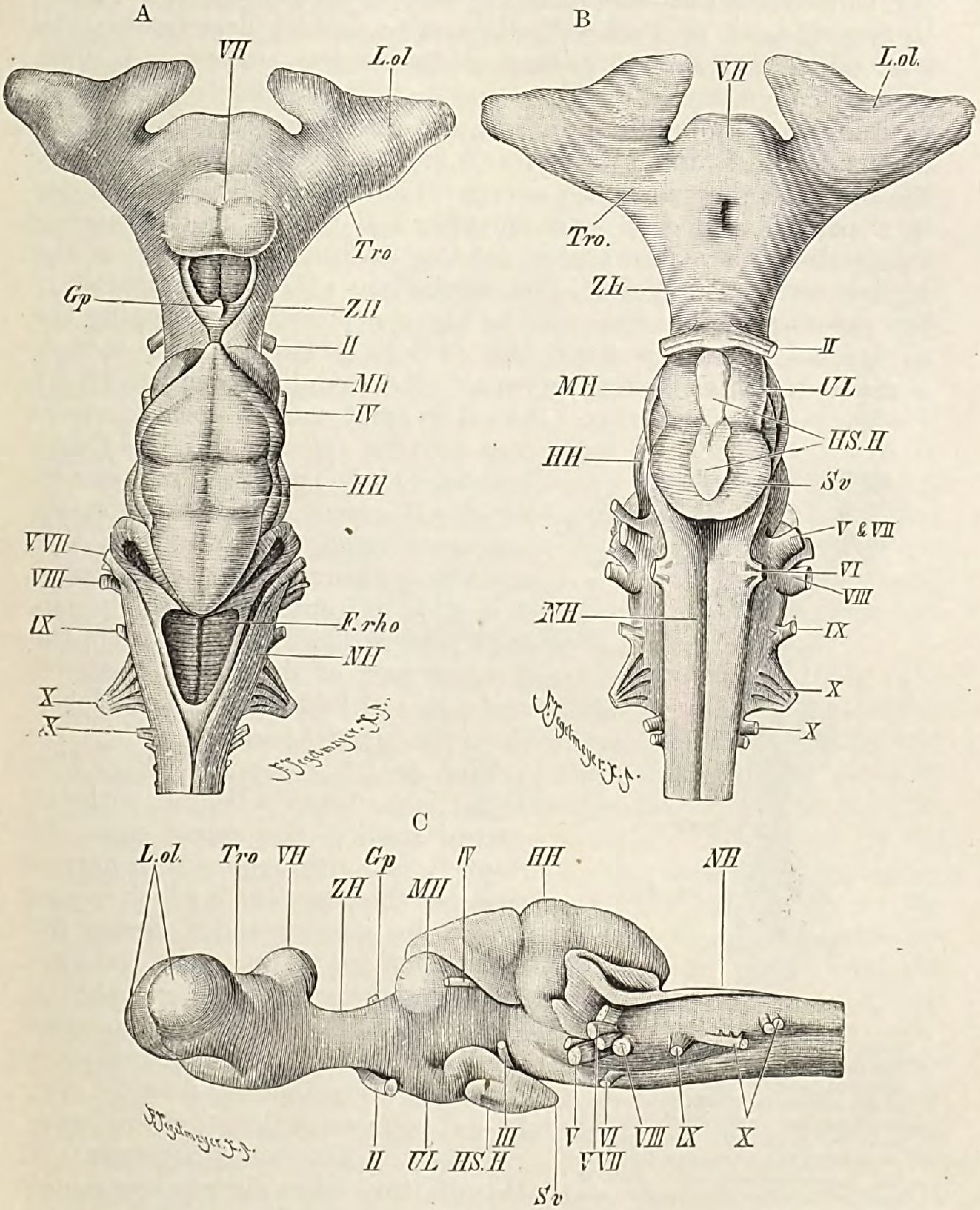


Fig. 775.—Brain of **Scyllium canicula.** A, dorsal view; B, ventral view; C, lateral view. *F. rho.* fossa rhomboidalis (fourth ventricle); *Gp*, epiphysis; *HH*, cerebellum; *HS. A*, hypophysis; *L. ol.* olfactory lobe; *MH*, mid-brain; *NH*, medulla oblongata; *Sv*, saccus vasculosus; *Tro*, olfactory peduncle; *UL*, lobi inferiores; *VH*, prosencephalon; *ZH*, diencephalon; *II*, optic nerves; *III*, oculomotor; *IV*, pathetic; *V*, trigeminal; *VI*, abducent; *VII*, facial; *VIII*, auditory; *IX*, glossopharyngeal; *X*, vagus. (From Wiedersheim.)

terminates in a slightly dilated extremity fixed to the membranous part of the roof of the skull. Projecting downwards from its

floor are two rounded bodies, the *lobi inferiores* (*UL*), which are dilated portions of the *infundibulum*; and attached to this, behind, is a thin-walled sac—the *pituitary body* or *hypophysis cerebri* (*HS*), having a pair of thin-walled vascular lateral diverticula—the *sacci vasculosi* (*S.v.*), and having on its ventral surface a median tubular body attached at its posterior end to the floor of the skull. In front of the infundibulum, and also on the lower surface of the diencephalon, is the *optic chiasma*, formed by the decussation of the fibres of the two optic nerves. The mid-brain (*MH*) consists of a pair of oval *optic lobes* dorsally, and ventrally of a band of longitudinal nerve-fibres corresponding to the *crura cerebri* of the higher vertebrate brain. The cerebellum (*HH*) is elongated in the antero-posterior direction, its anterior portion overlapping the optic lobes, and its posterior the medulla oblongata. Its surface is marked with a few fine grooves. The medulla oblongata (*NH*), broad in front, narrows posteriorly to pass into the spinal cord. The *fourth ventricle* (*F. rho.*) is a shallow space on the dorsal aspect of the medulla oblongata covered over only by a thin vascular membrane, the *choroid plexus*: it is wide in front and gradually narrows posteriorly. At the sides of the anterior part of the fourth ventricle are a pair of folded ear-shaped lobes, the *corpora restiformia*.

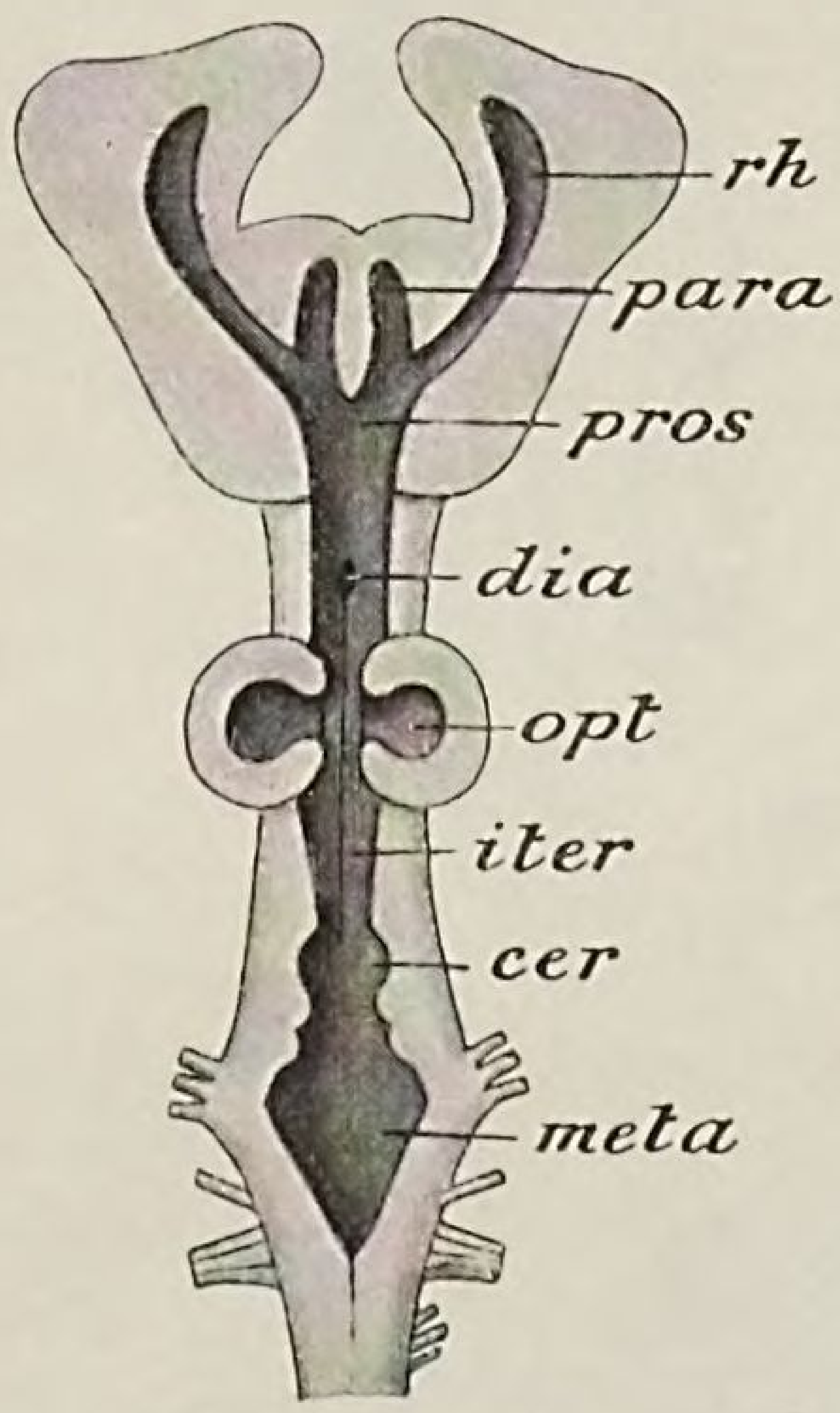


FIG. 776.—**Chiloscyllium.** The brain viewed from the dorsal side, the roofs of the various ventricles removed so as to show the relations of the cavities (semi-diagrammatic). *cer*, dilatation from which the epicœle is given off; *dia.* diacœle, pointing to the opening leading into the infundibulum; *iter.* iter or passage between the diacœle and the metacœle; *meta.* metacœle; *opt.* optocœle; *para.* paracœle; *pros.* prosocœle; *rh.* rhinocœle.

The fourth ventricle (Fig. 776, *meta.*) is continuous behind with the central canal of the spinal cord. In front it is continuous with a narrow passage, the *iter* (*iter.*), which opens anteriorly into a wider space, the *diacœle* or *third ventricle* (*dia.*) occupying the interior of the diencephalon. From this opens in front a median *prosocœle*, which gives off a pair of *paracœles* (*para.*) extending into the two lateral portions of the prosencephalon.

From the anterior enlargements of the olfactory lobes already mentioned spring numerous fibres which constitute the first pair of cranial nerves and enter the olfactory capsules. From the optic chiasma the two optic nerves (Fig. 775, *II*) run outwards through the optic foramina into the orbits, each perforating the sclerotic of the corresponding eye and terminating in the retina. The third, fourth, and sixth pairs of nerves have

the general origin and distribution which has already been described as universal in the Craniata (p. 97).

The *trigeminal* (Fig. 775, *V*) arises in close relation to the facial. As it passes into the orbit it swells into a ganglion—the *Gasserian*. Its chief branches are three in number. The first given off is the *superficial ophthalmic* (Fig. 777, *oph. V*), which runs forwards through the orbit above the origin of the recti muscles, and in very close relation with the ophthalmic branch of the facial. Anteriorily it breaks up into branches for the supply of the mucous canals of the dorsal surface of the snout. The main trunk of the nerve then runs forwards and outwards across the floor of the orbit, and divides into two branches the *maxillary* and *mandibular* or second and third divisions of the trigeminal. The former (*mx. V*) supplies the mucous canals of the ventral surface of the snout; the latter (*mnd. V*) supplies the muscles of the lower jaw.

A nerve of considerable size,—the *ophthalmicus profundus*—arises in front of the root of the trigeminal, with which it is in close communication. After leaving the cranial cavity it enlarges into a small ganglion, and runs forwards over the external rectus muscle and under the superior rectus, and perforates the pre-orbital process to end in the integument of the snout. Among other branches it gives off ciliary branches to the iris: these are joined by the ciliary branches of the oculomotor.

Of the branches of the facial, the *superficial ophthalmic* runs through the orbit in close relation to the superficial ophthalmic branch of the trigeminal, and is distributed to the ampullæ and mucous canals of the snout region; the *buccal* runs forwards in intimate relation with the maxillary division of the trigeminal, and breaks up into branches which are mainly distributed to the ampullæ and canals of the region of the snout; the *palatine* (*pl. VII*) runs to the roof of the mouth; the main body of the nerve—hyomandibular nerve (*hy. mnd. VII*)—then runs outwards close to the edge of the hyomandibular cartilage and behind the spiracle, eventually becoming distributed to the muscles between the spiracle and the first branchial cleft.

The *eighth* or *auditory* nerve passes directly into the internal ear, and breaks up into branches for the supply of its various parts. The *glossopharyngeal* (*gl. ph.*) perforates the posterior part of the auditory region of the skull, and, after it reaches the exterior, passes to the first branchial cleft, where it bifurcates, one branch passing to the anterior, and the other to the posterior wall of the cleft. The last nerve of the series—the *pneumogastric* or *vagus* (*vag.*)—is a large nerve which emerges from the skull by an aperture situated between the auditory region and the foramen magnum. It first gives off a series of four *branchial* branches, each of which bifurcates to supply the anterior and posterior borders of the last four branchial clefts. It then gives off a *lateral* nerve

(*lat. vag.*), which runs along beneath the lateral line to the posterior end of the body. The rest of the nerve runs backwards to divide into *cardiac* branches for the heart and *gastric* branches for the stomach.

The spinal cord is a cylindrical cord which extends from the foramen magnum, where it is continuous with the hind brain, backwards throughout the length of the neural canal enclosed by

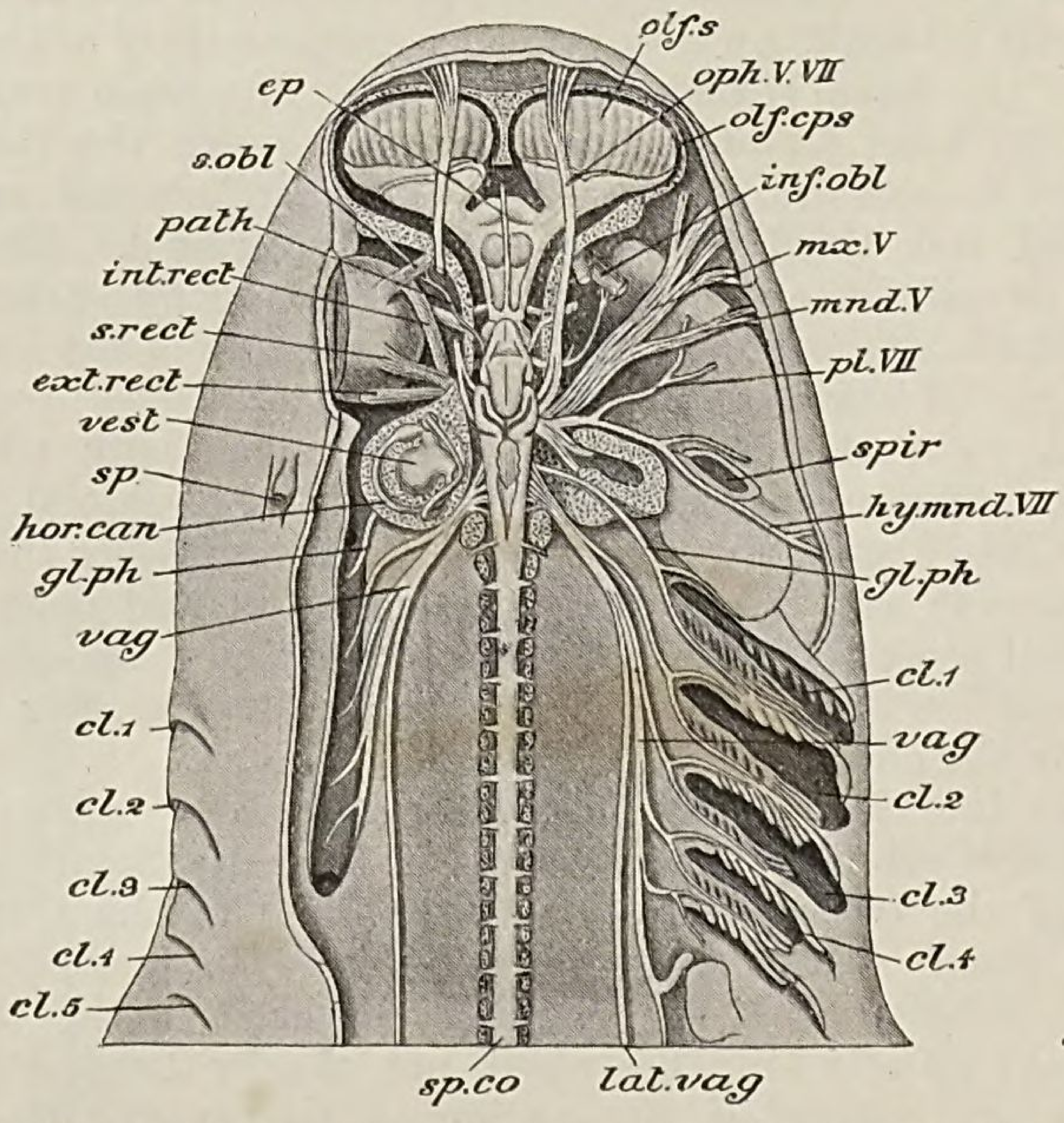


FIG. 777.—**Scyllium catulus.**—Dissection of the brain and spinal nerves from the dorsal surface. The right eye has been removed. The cut surfaces of the cartilaginous skull and spinal column are dotted. The ophthalmicus profundus and the buccal branch of the facial are not represented; *cl.*$_1$—*cl.*$_5$, branchial clefts; *ep.* epiphysis; *ext. rect.* external rectus muscle of the eye-ball; *gl. ph.* glossopharyngeal; *hor. can.* horizontal semicircular canal; *hy. mnd. VII.*; hyomandibular portion of the facial; *inf. old.* inferior oblique muscle; *int. rect.* internal rectus muscle; *lat. vag.* lateral branch of vagus; *mx. V.* maxillary division of the trigeminal; *olf. cps.* olfactory capsule; *olf. s.* olfactory sac; *oph. V. VII.* superficial ophthalmic branches of trigeminal and facial; *path*, fourth nerve; *pl. VII.* palatine branch of facial; *sp. co.* spinal cord; *spir.* spiracle; *s. rect.* superior rectus muscle; *s. olb.* superior oblique; *vag.* vagus; *vest.* vestibule. (From Marshall and Hurst.)

the neural arches of the vertebræ. As in the Craniata in general (see p. 92), it has dorsal and ventral longitudinal fissures and a narrow central canal, and gives origin to a large number of paired spinal nerves, each arising from it by two roots.

Organs of Special Sense.—The *olfactory organs* are rounded chambers enclosed by the cartilage of the olfactory capsules of the skull, and opening on the exterior by the external nares on the ventral surface of the head. The interior has its lining membrane raised up into a number of close-set ridges running out from

a median septum. The fibres of the olfactory nerves terminate in cells of the epithelium covering the surface of these ridges.

The *eye* has the general structure already described as characterising the Craniata in general (p. 103). The sclerotic is cartilaginous, the choroid has a shining metallic internal layer or *tapetum*, and the lens is spherical. The eyeball is attached to the inner wall of the orbit by a cartilaginous stalk. There are the usual eye-muscles, the two *obliques* situated anteriorly, the four *recti* posteriorly. There are no eyelids.

The ear consists only of the *membranous labyrinth* equivalent to the internal ear of higher Craniata, the middle ear and the outer ear being absent. The membranous labyrinth consists of the *vestibule* and three *semicircular canals*. The former, which is divided into two parts by a constriction, communicates by a narrow passage—the *aqueductus vestibuli*—with the exterior, in the position already mentioned. Of the three semicircular canals, the anterior and posterior are vertical and the external horizontal, as in Craniata in general. Each has an ampulla, that of the anterior and external canals situated at their anterior ends, and that of the posterior canal, which is the largest of the three, and forms an almost complete circle, at its posterior end. In the fluid (*endolymph*) in the interior of the vestibule are suspended, in a mass of gelatinous connective tissue, numerous minute calcareous particles or *otoliths*, giving it a milky character.

The *mucous canals* of the integument contain special nerve-endings, and doubtless function as organs of some special sense. The same probably holds good of a number of minute canals situated on the anterior portion of the trunk, and on the head, being particularly numerous in the neighbourhood of the snout. These are dilated internally into vesicles, the *ampullæ*, provided with special nerve-endings.

Urino-genital Organs.—In the female there is a single ovary (Fig. 773, *ov.*), an elongated, soft, lobulated body, lying a little to the right of the middle line of the abdominal cavity, attached by a fold of peritoneum, the *mesoarium*. On its surface are rounded elevations of various sizes, the *Graafian follicles*, each containing an ovum of a bright yellow colour. There are two oviducts (Müllerian ducts) entirely unconnected with the ovaries. Each oviduct (Fig. 773, *ovd.*; Fig. 778) is a greatly elongated tube extending throughout the entire length of the abdominal cavity. In front the two unite behind the pericardium to open into the abdominal cavity by a wide median aperture (*abd. ap.*). At about the point of junction of the middle and anterior thirds is a slight swelling marking the position of the *shell-gland* (*sh. gld.*). The posterior part dilates to form a wide chamber, and in Scyllium the two unite to open into the cloaca by a common aperture situated just behind the

opening of the rectum, while in Chiloscyllium they remain distinct and have separate cloacal openings. Each kidney consists of two parts, anterior and posterior. The former (Fig. 773, *r. meson.*) is a long narrow ribbon of soft reddish substance, which runs along throughout a great part of the length of the body-cavity at the side of the vertebral column, covered by the peritoneum. The posterior portion (*r. metan.*) is a compact, lobulated, dark-red body, lying at the side of the cloaca, continuous with the anterior portion; like the latter, it is covered over by the peritoneum. Both portions have their ducts. Those of the anterior are narrow tubes, which run over its ventral surface and become dilated behind to form a pair of elongated chambers, the *urinary sinuses* (Fig. 779, *ur. sin*), which unite into a median sinus (*med. ur. sinus.*), opening into the cloaca by a median aperture situated on a papilla, the *urinary papilla.* The ducts of the posterior portion, the *ureters*, which are usually from four to six in number, open into the urinary sinuses.

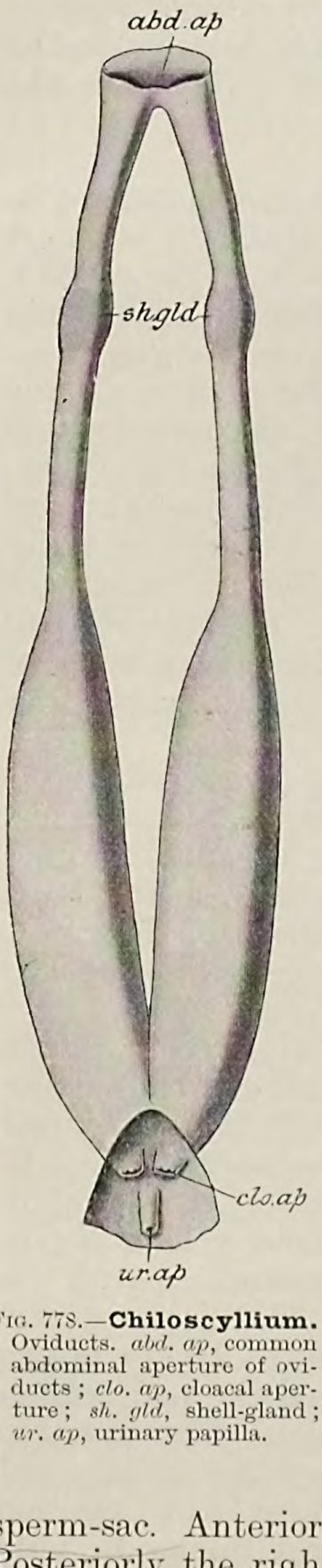


FIG. 778.—**Chiloscyllium.** Oviducts. *abd. ap*, common abdominal aperture of oviducts; *clo. ap*, cloacal aperture; *sh. gld*, shell-gland; *ur. ap*, urinary papilla.

In the male there are two elongated, soft, lobulated *testes*, each attached to the wall of the abdominal cavity by a fold of peritoneum—the *mesorchium*. From each testis efferent ducts pass to the anterior end of a long, narrow, strap-shaped body, which corresponds to the anterior portion of the kidney in the female. This is the *epididymis*, the duct of which is a convoluted tube running along the entire length of the mesonephros, and where it leaves the latter posteriorly becoming a wide tube—the *vas deferens* or spermiduct—which opens into a special median compartment of the cloaca, the *urino-genital sinus.* Posteriorly the spermiduct dilates to form a wide thin-walled sac, the *vesicula seminalis.* Closely applied to the latter is a thin-walled elongated sac, the sperm-sac. Anteriorly the sperm-sac narrows to a blind extremity. Posteriorly the right and left sperm-sacs combine to form the urino-genital sinus. The posterior part of the kidney has the same character as in the female; its ducts, usually five in number

on each side, open into the urino-genital sinus. The latter has a median aperture into the general cavity of the cloaca situated on the summit of a prominent *urino-genital papilla*. The oviducts (Mullerian ducts) of the female are represented in the male by rudiments of their anterior portions. The entire kidney is sometimes regarded as a mesonephros, but the posterior portion, developed entirely behind the part which is converted in the male into the epididymis, and having its own ducts, is sometimes

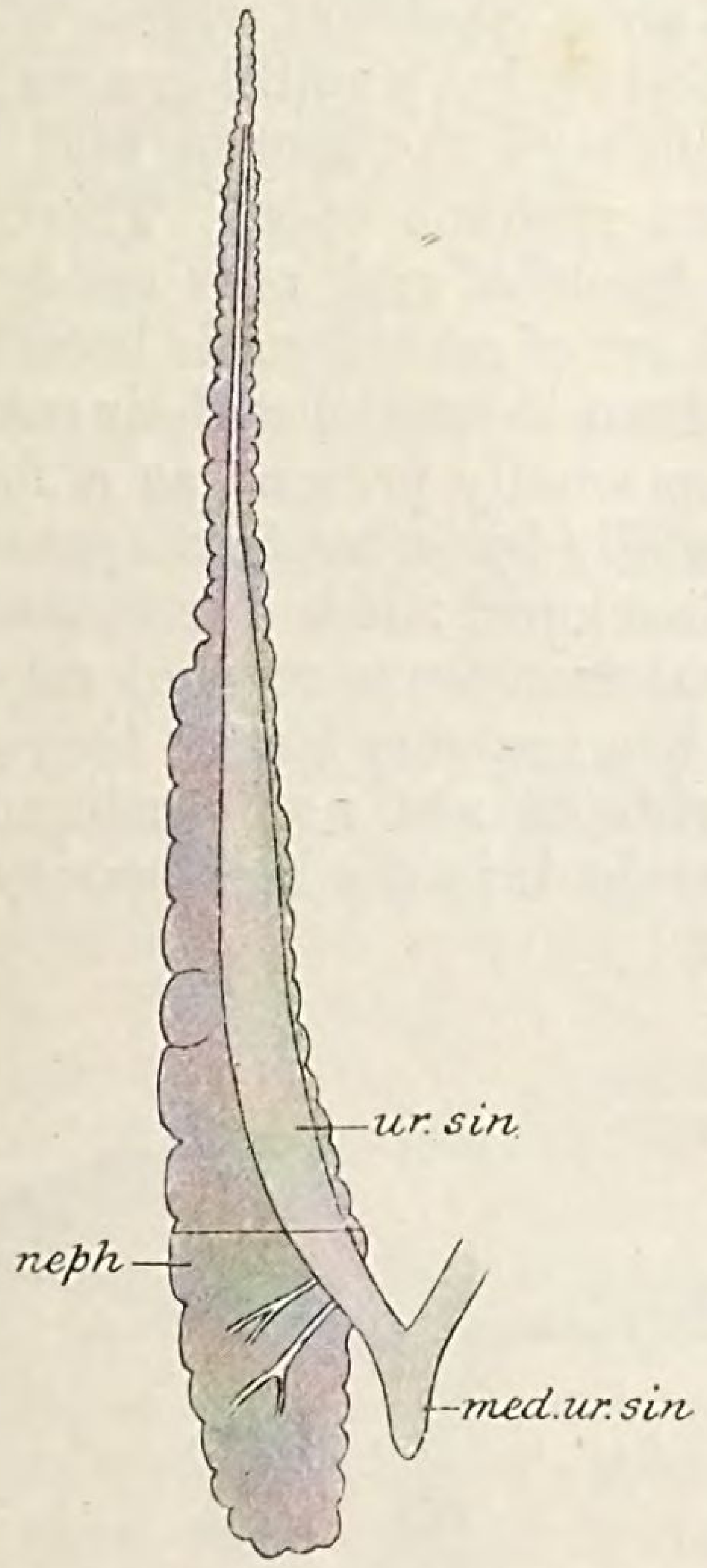


FIG. 779.—**Chiloscyllium.** Right kidney and urinary sinus of female. *med. ur. sinus*, median urinary sinus; *neph*, kidney; *ur. sinus*, right urinary sinus.

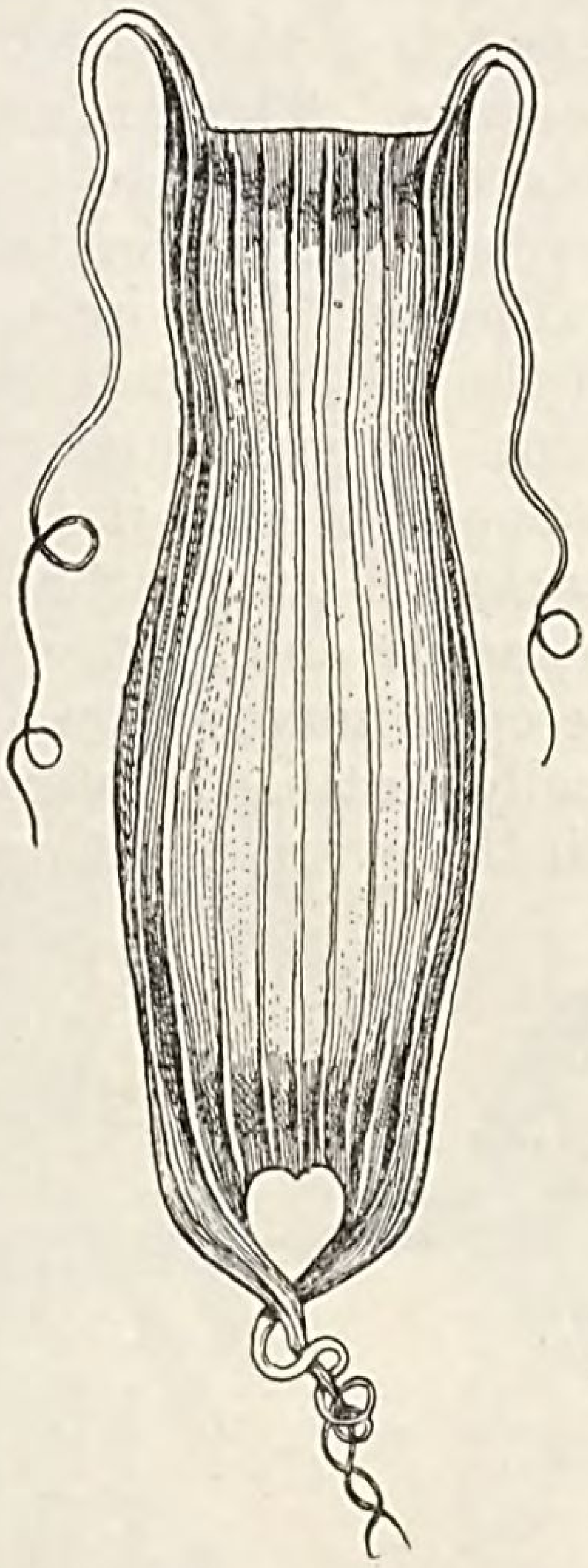


FIG. 780.—**Dog-fish,** egg-case. (After Dean.)

looked upon as corresponding to the metanephros of the higher Vertebrates.

The ripe ovum, rupturing the wall of its Graafian follicle, escapes into the abdominal cavity, whence it reaches the interior of one of the oviducts; there it becomes fertilised by sperms received from the male in the act of copulation, and then becomes enclosed in a chitinoid case or shell (Fig. 780) secreted by the shell-gland.

2.—Distinctive Characters and Classification.

The Elasmobranchii are Pisces in which the cartilaginous cranium is never ossified by cartilage-bones, and in which membrane-bones are not developed in connection either with the cranium or the pectoral arch. The skull is hyostylic, except in some of the Protoselachii, in which it is amphistylic. The dermal fin-rays are horny; they are supported by cartilaginous pterygiophores which are never very numerous. The pelvic arch is a distinct cartilage. There is nearly always an exoskeleton, which, when present, is of the placoid type. The intestine has a spiral or a scroll-like valve. There is a cloaca into which both the rectum and the ducts of the urinary and reproductive systems open. There is never an operculum in recent Elasmobranchs, and only rarely in fossil forms. The inter-branchial septa are of considerable breadth, and the gill-filaments are attached to them throughout their entire extent. A spiracular gill is only exceptionally present as a fully developed organ; it is represented usually by a vestige (*pseudobranch*). A conus arteriosus is always developed; it is rhythmically contractile, and in its interior are several transverse rows of valves. The optic nerves form a chiasma. The ova are very large: they are usually fertilised internally. The oviducts are not continuous with the ovaries, but open by wide mouths into the body-cavity.

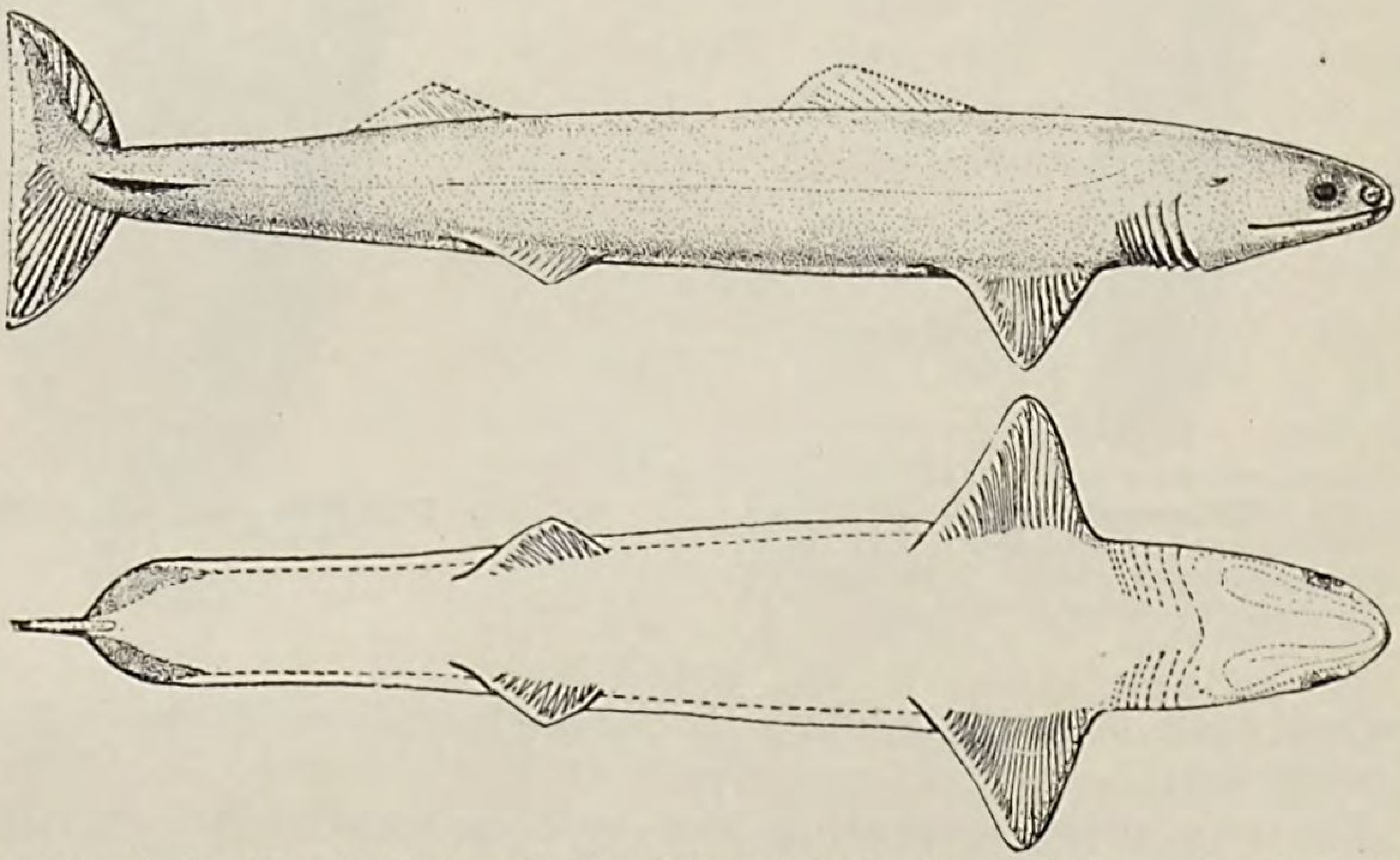


Fig. 781.—Restoration of **Cladoselache fyleri,** lateral and ventral views. (Restored, after Dean.)

Order 1.—Cladoselachea.

Extinct Shark-like Elasmobranchs in which both pectoral and pelvic fins had much wider bases of attachment than in existing

forms. The notochord was persistent: there were no intercalary cartilages. The caudal fin was strongly heterocercal. Claspers were absent. The gill-openings were apparently protected by a fold of skin. The teeth were of the nature of placoid denticles. The lateral line was represented by an open groove.

This order comprises only one known representative—*Cladoselache*—from the lower Carboniferous rocks of America.

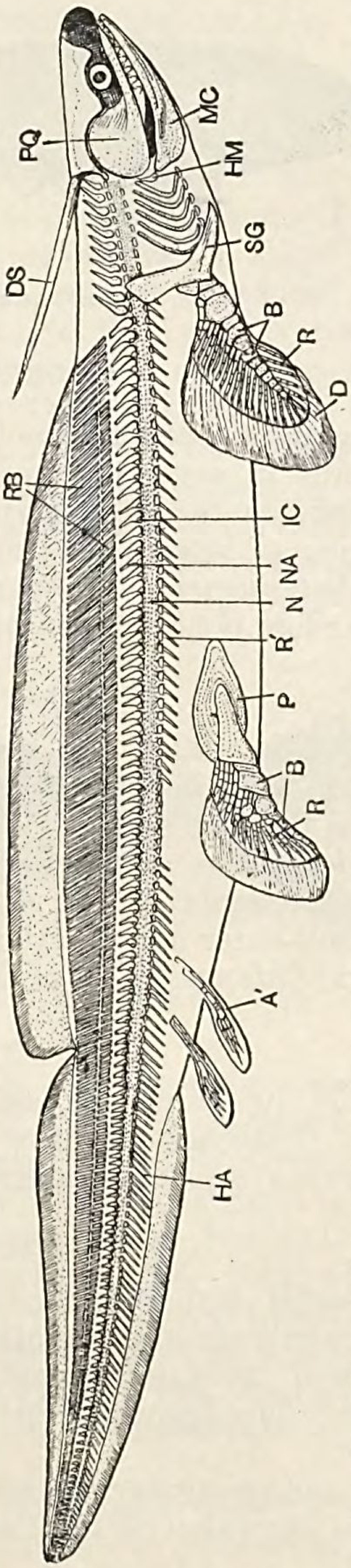


FIG. 782.—**Pleuracanthus ducheni,** restored. *A'*, ventral fin; *B*, basal fin-cartilages; *D*, dermal margin of fin; *D. S.* dermal fin-spine; *H. A.* hæmal arches; *HM.* hyomandibular; *I. C.* inter-neural plates; *M. C.* Meckel's cartilage; *N.* notochord; *NA*, neural process and spine; *P.* pelvic cartilage[1]; *P. Q.* palato-quadrate; *R.* radial fin-cartilages; *R'.* rib; *S. G.* shoulder-girdle. (From Dean.)

[1] It is possible that this structure may be a *coprolite* or fossilized mass of fæcal matter.

ORDER 2.—PLEURACANTHEA.

Extinct Shark-like Elasmobranchs in which the skeleton of the pectoral fin was constructed on the type of the *archipterygium*, *i.e.* consisted of an elongated segmented central axis bearing two rows of jointed rays. The notochord was persistent, but intercalary cartilages were present. The caudal fin was diphycercal. Claspers were present. There was no opercular fold, and the teeth resembled those of other Elasmobranchs. There were no placoid scales, but the skull was protected by roofing dermal bones.

This order, like the last, includes only one satisfactorily known genus—*Pleuracanthus*—of Carboniferous and Permian age.

ORDER 3.—ACANTHODEA.

Extinct Elasmobranchs having the anterior margin of each fin supported by a stout spine. The tail was heterocercal. There were probably membrane-bones on the roof of the skull. The

teeth were few and large. The lateral line was in the form of an open groove.

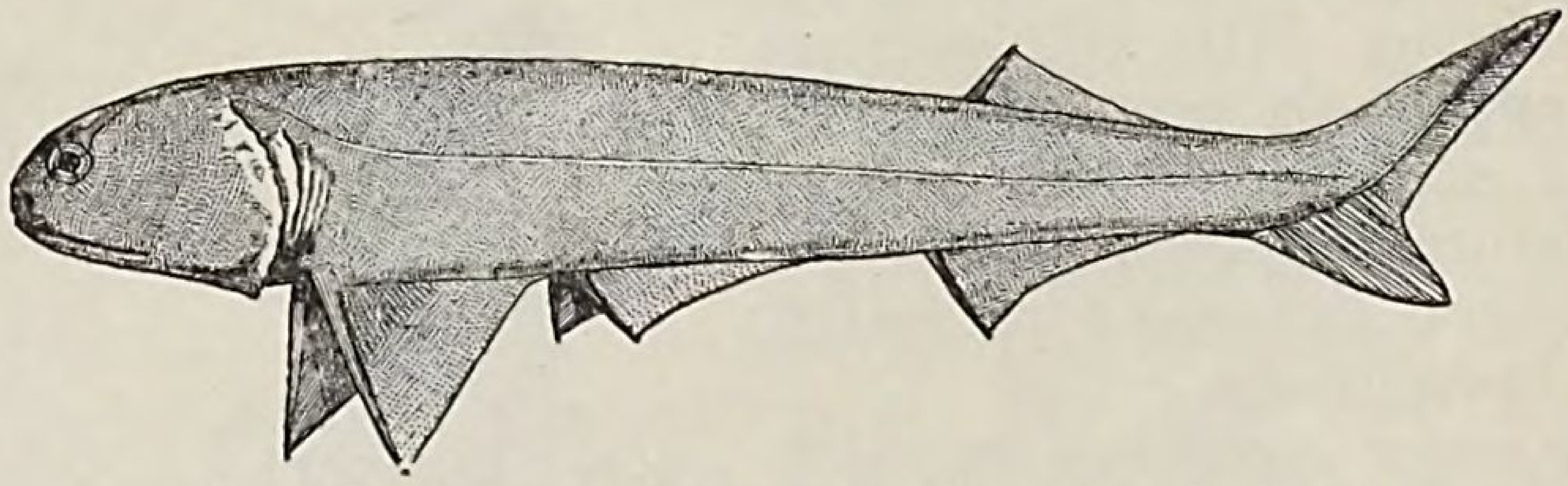


FIG. 783.—**Acanthodes wardi.** (Restored, after Dean.)

ORDER 4.—SELACHII.

Living and extinct Elasmobranchs in which the skeleton of the paired fins is never of the nature of an archipterygium. The notochord is more or less completely replaced by vertebræ, and there is a series of intercalary cartilages. The caudal fin is nearly always heterocercal. Claspers are always developed. A distinct opercular fold is never present.

Sub-Order a.—Protoselachii.

Selachii in which the spinal column is unossified, and the centra are very imperfectly developed; there are more than five branchial arches. The palato-quadrate develops, except in *Chlamydoselachus*, a process by which it articulates with the post-orbital region of the skull.

This sub-order includes the *Notidanidæ* (*Hexanchus* and *Heptanchus*), and *Chlamydoselachus*, as well as, probably, many fossil forms.

Sub-Order b.—Euselachii.

Selachii in which the spinal column is partly or completely ossified. There are only five branchial arches. The palato-quadrate has no post-orbital articulation with the skull.

Section α.—Squalida.

Euselachii with fusiform body and well-developed caudal fin. The pectorals are of moderate size. A ventral fin is present. The vertebræ of the anterior part of the spinal column are not fused together. The branchial apertures and the spiracle are situated laterally.

This section comprises all the recent Sharks and Dog-fishes, with the exception of the Protoselachii.

Section β.—Rajida.

Euselachii with dorso-ventrally compressed body, and, usually, feebly developed caudal fin. The pectorals are of great size, the

pelvics usually small. A ventral fin is usually absent. The vertebræ of the anterior region are fused together. The branchial apertures are ventral, the spiracles dorsal.

This section comprises all the recent and extinct Rays (Skates, Thorn-backs, Sting-Rays, Electric Rays, Saw-fish Rays).

3.—General Organisation.

External Characters.—In general shape the Sharks (Fig. 784), for the most part, are somewhat fusiform and slightly compressed laterally. In the Rays (Fig. 785), on the other hand, there is great dorso-ventral compression. The head is in many cases produced forwards into a long rostrum, which is of immense length and bordered with triangular teeth in the Saw-fish Shark (*Pristiophorus*) and Saw-fish Ray (*Pristis*). In the Hammerhead Shark the anterior part of the head is elongated transversely.

There are well-developed median and paired fins. The caudal fin is well developed, and, as a rule, strongly heterocercal in the

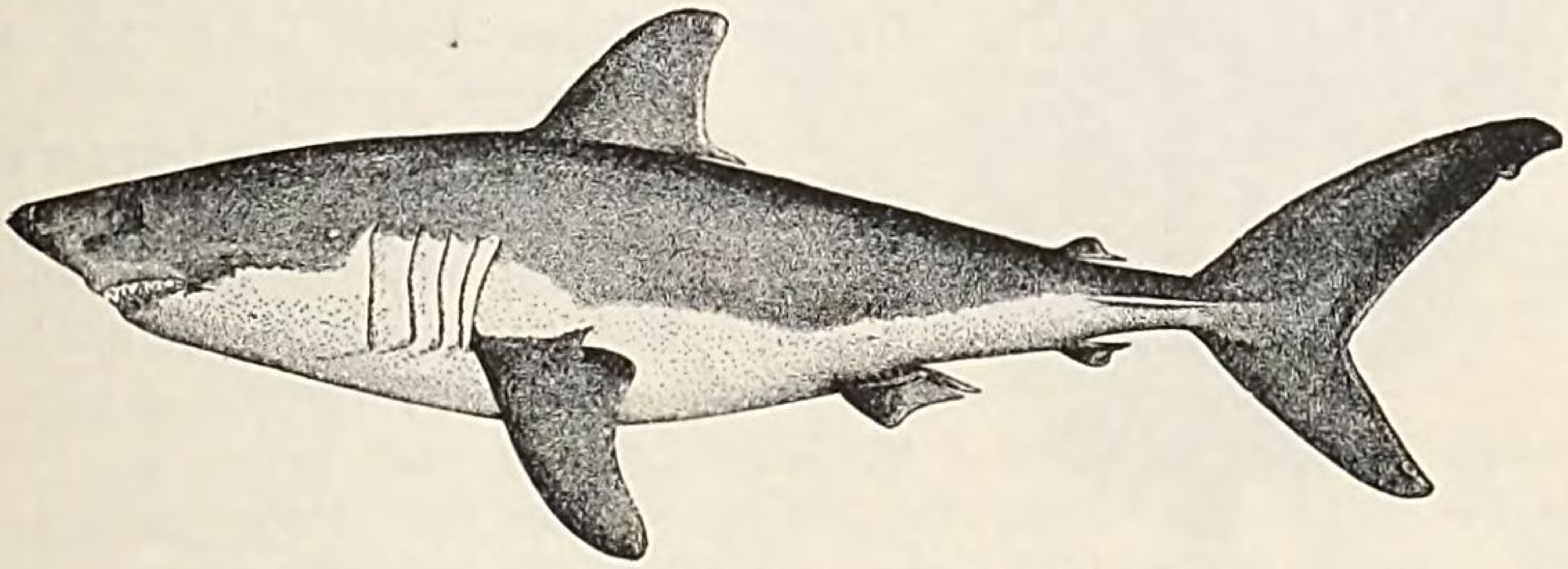


Fig. 784.—**Shark** (*Lamna cornubica*). (From Dean's *Fishes*.)

Sharks and Shark-like Rays, feebly developed in most of the latter group. The dorsal and ventral fins are large in the Sharks, the former completely divided into two: in the Rays the dorsal fin is usually small, and the ventral absent. The paired fins are very differently developed in the two groups. In the Sharks both pairs are well developed, the pectoral being the larger. In the Rays the pectoral fins are extremely large, very much larger than the pelvic, fringing the greater part of the length of the flattened body, and becoming prolonged forwards on either side and even in front of the head, so that the animal presents the appearance of a broad fleshy leaf.

In all recent Elasmobranchs the male has, connected with the pelvic fins, a pair of grooved appendages—the *claspers* or *pterygopodia*—which subserve copulation.

The mouth is situated on the ventral surface of the head, usually a considerable distance from the anterior extremity. In front of

each angle of the mouth on the ventral surface is the opening of one of the olfactory sacs, each of which is connected by a groove—the naso-buccal groove—with the mouth-cavity. Behind the mouth, on the dorsal surface in the Rays, and at the side in the Sharks, is the spiracle. Along the sides of the neck in the Sharks, and on the ventral surface in the Rays, is on either side a row of slit-like apertures—the branchial slits or branchial clefts. These are usually five in number on each side; but in *Hexanchus* and *Chlamydoselachus* there are six, and in *Heptanchus* seven. In *Chlamydoselachus* a fold comparable to a rudimentary operculum extends back over the first branchial cleft, and is continuous across the middle line ventrally; in the remainder of the sub-class no such structure is represented. A large cloacal opening is situated just in front of the root of the tail, and a pair of small openings placed in front of it—the *abdominal pores*—lead into the abdominal cavity.

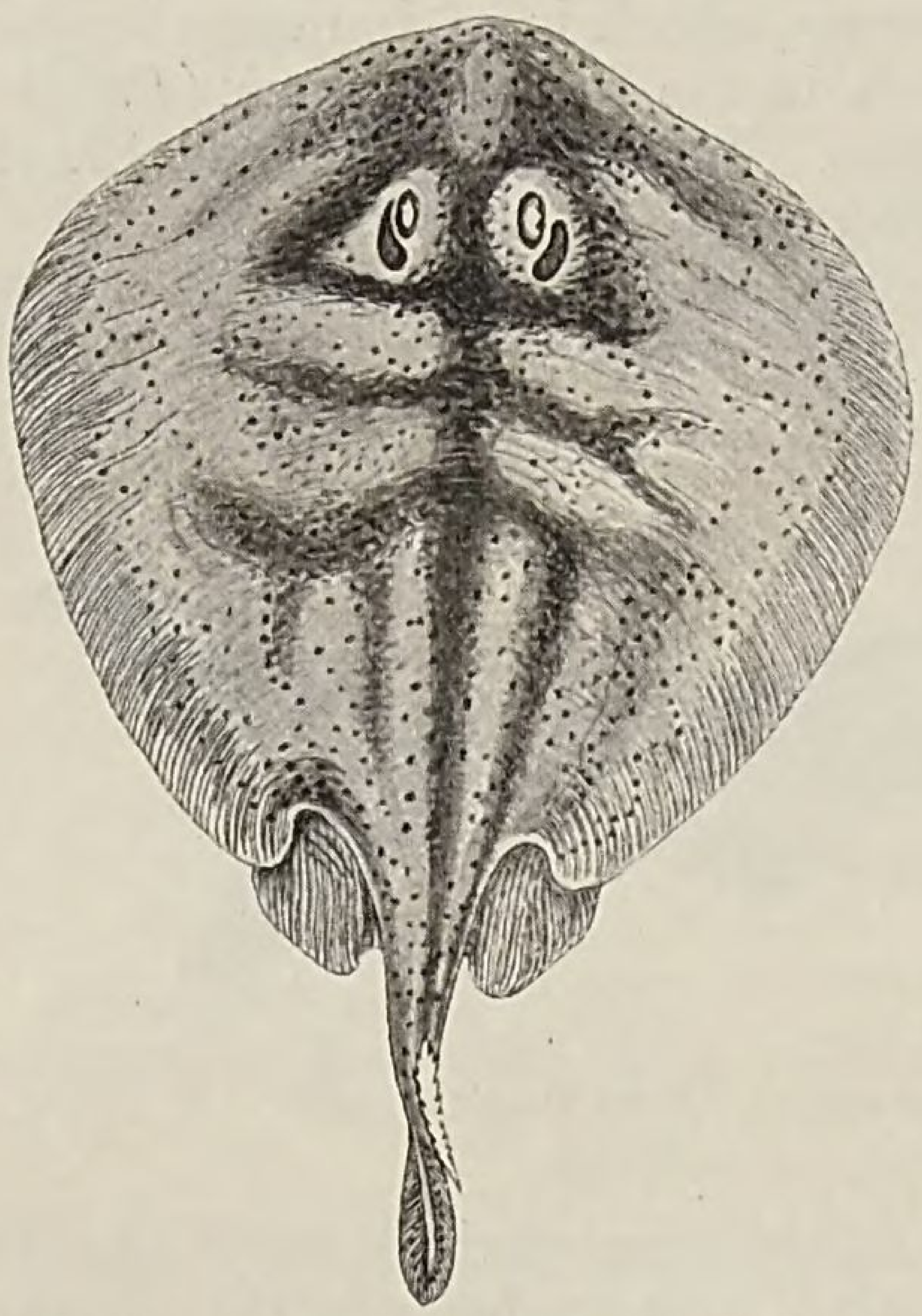


Fig. 785.—**Sting-Ray** (*Urolophus cruciatus*). (After Günther.)

When the **integument** develops any hard parts, as is the case in the majority of the Elasmobranchs, they take the form, not of regular scales, as in most other fishes, but of numerous hard bodies which vary greatly in shape, are usually extremely minute, but are in some cases developed, in certain parts of the surface, into prominent tubercles or spines. When these hard bodies are, as is commonly the case, small and set closely together in the skin, they give the surface very much the character of a fine file; and the skin so beset, known as "shagreen," is used for various polishing purposes in the arts. This is the *placoid* form of exoskeleton, to which reference has been already made. Each of the hard bodies has the same structure as a tooth, being composed of dentine, capped with enamel, and supported on a bony base, representing the cement or *crusta petrosa* of the tooth.

The **skeleton** is composed of cartilage, with, in many cases, deposition of bony matter in special places—notably in the jaws and the vertebral column. The entire spinal column may be nearly completely cartilaginous (*Hexanchus* and *Heptanchus*), but usually

the centra are strengthened by radiating or concentric lamellæ of bone; or they may be completely ossified. They are deeply amphicœlous, the remains of the notochord persisting in the large inter-central spaces. *Intercalary pieces* (Fig. 787, *Ic.*) are interposed between both superior and inferior arches. In the Rays (Fig. 788) the anterior part of the spinal column becomes converted into a continuous solid cartilaginous and bony mass—the *anterior vertebral plate* (*a.v.p.*) As in Fishes in general, two regions are distinguishable in the spinal column—the *præ-caudal* and the *caudal*, the latter being distinguished by the possession of inferior or hæmal arches. In the præ-caudal region short ribs may be developed, but these are sometimes rudimentary or entirely absent. In the Sharks pterygiophores, sometimes jointed, fused at their bases with the hæmal spines, support the ventral lobe of the caudal fin, and the dorsal lobe of the same fin is supported by a series of pterygiophores resembling produced neural spines, but only secondarily related to the spinal column and sometimes also divided by joints. The dorsal and ventral fins are sometimes supported by similar pterygiophores; but in many cases the cartilaginous supports of these fins consist, in whole or in part, of expanded plates of cartilage.

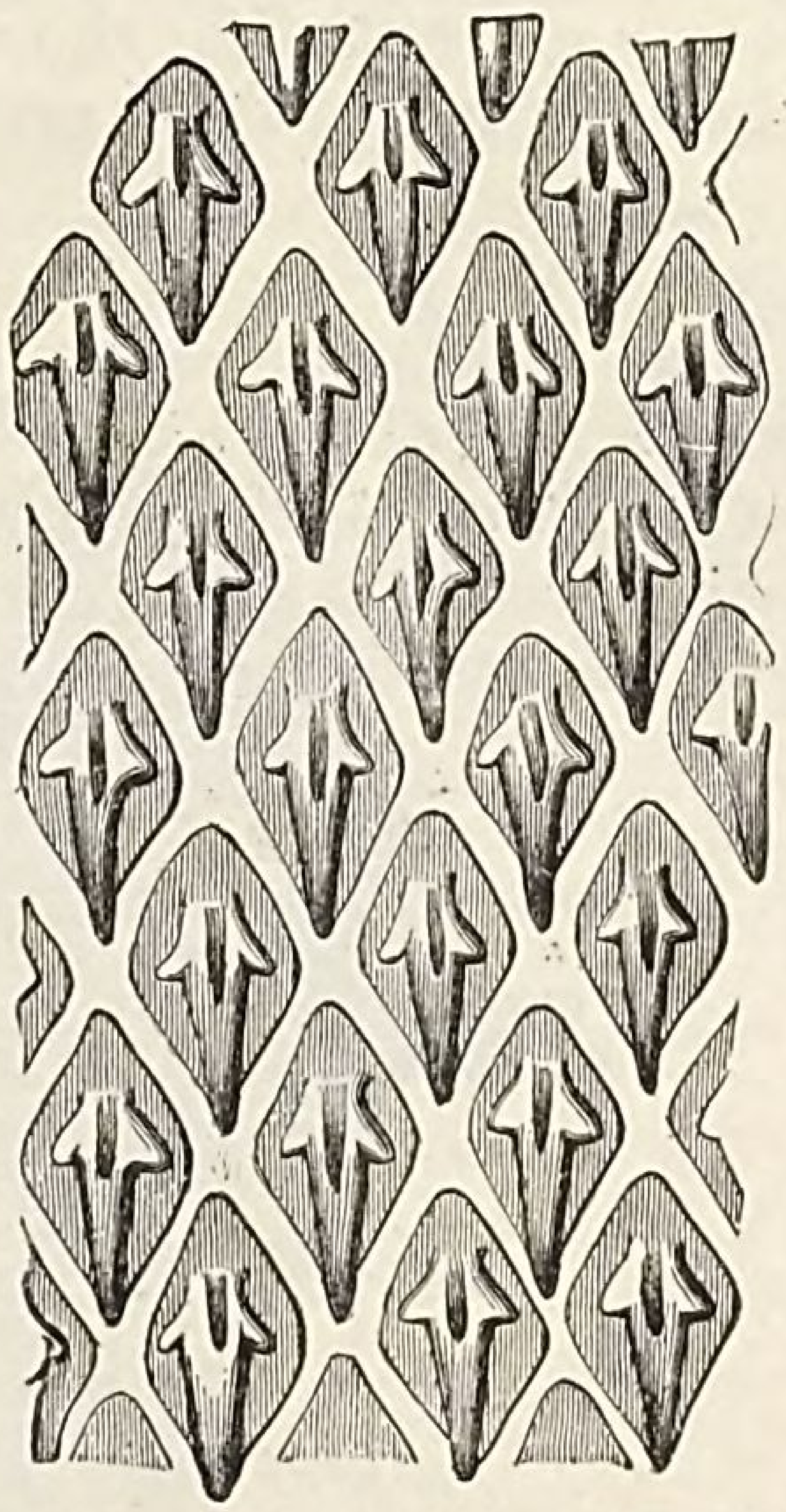


FIG. 786.—Dermal denticles of **Centrophorus calceus,** slightly magnified. (From Gegenbaur's *Comparative Anatomy.*)

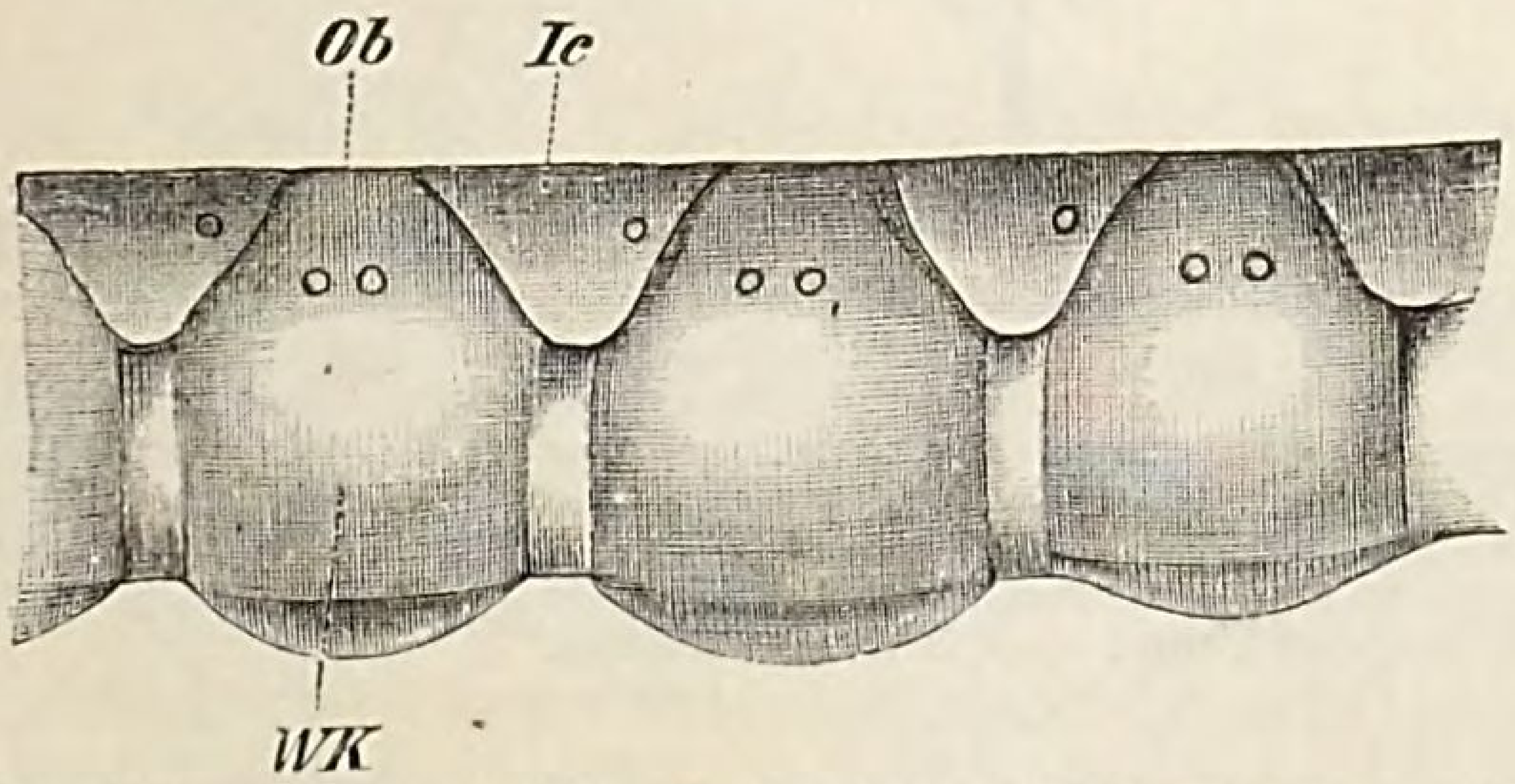


FIG. 787.—Portion of the spinal column of **Scymnus.** *Ic.* intercalary cartilages; *Ob*, neural arches; *WK*, centra. (From Wiedersheim.)

The **skull** is an undivided mass of cartilage, hardened, in many cases, by deposition of osseous matter, but not containing any separate bony elements. It consists of a cartilaginous case for the protection of the brain and the organs of special sense. The structure of this cartilaginous brain-case as it occurs in the Dog-fish has

already been described. The main differences observable in the different families are connected with the size and form of the rostrum. In the Rays the lower lip of the foramen magnum is deeply excavated for the reception of a short process, the so-called *odontoid process,* which projects forwards from the anterior vertebral

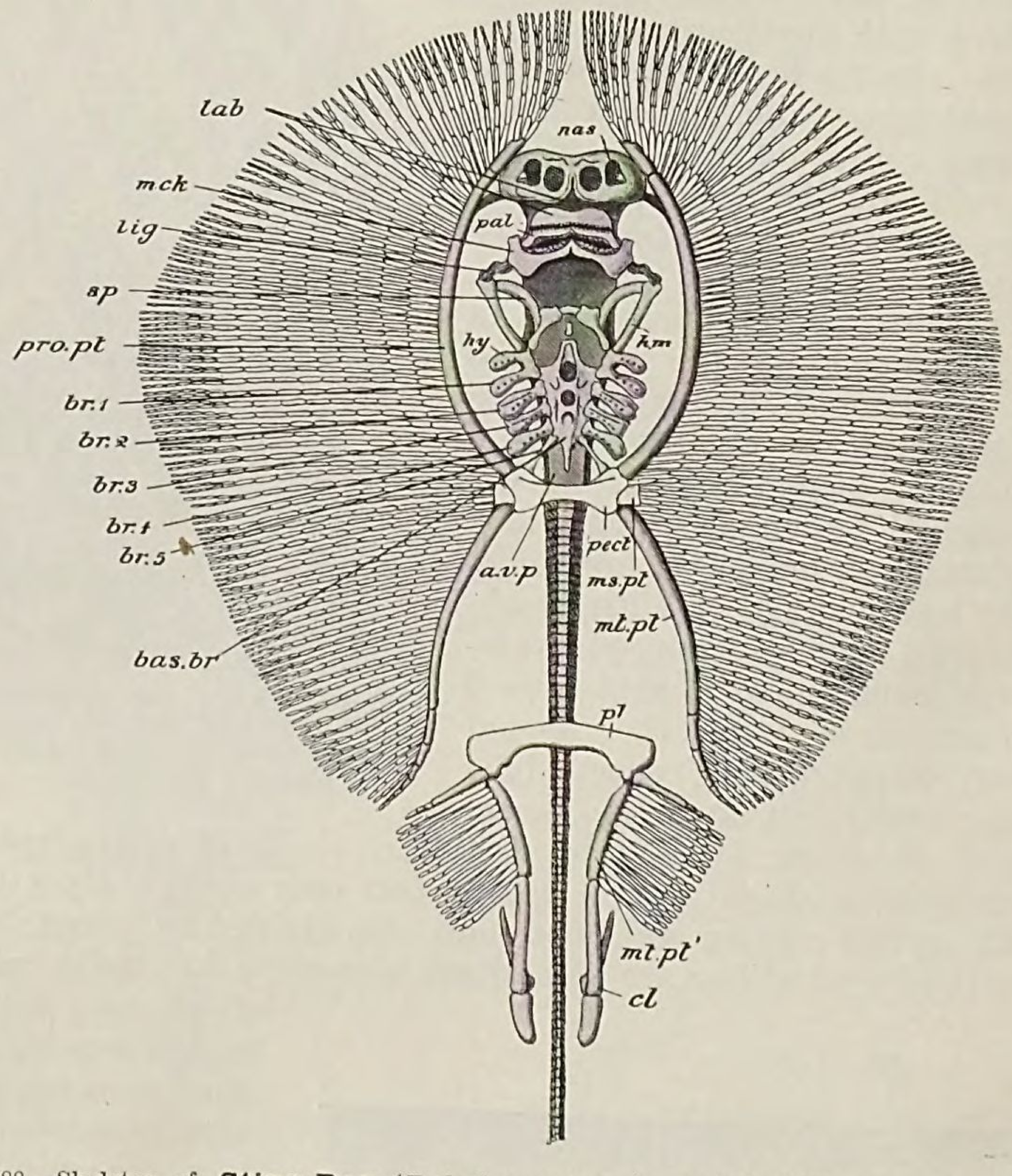


FIG. 788.—Skeleton of **Sting-Ray** (*Urolophus testaceus*), ventral view. *a. v. p.* anterior vertebral-plate; *bas. br.* basi-branchial plate; *br.*1—*br.*5 branchial arches. The branchial rays are represented as having been removed, the round dots indicate their articulations with the arches. *cl.* skeleton of clasper; *h. m.* hyomandibular; *hy.* hyoid arch; *lab.* labial cartilage; *lig.* ligament connecting the hyomandibular with the palato-quadrate and Meckel's cartilage; *Mck.* Meckel's cartilage; *ms. pt.* mesopterygium; *mt. pt.* metapterygium of pectoral fin; *mt. pt'.* metapterygium of pelvic fin; *nas.* nasal cartilage; *pal.* palato-quadrate; *pect.* pectoral arch; *pl.* pelvic arch; *pro. pt.* propterygium; *sp.* spiracular cartilage.

plate, and on either side of this is an articular surface—the occipital condyle—for articulation with corresponding surfaces on that plate. In the Sharks the skull is fused with the spinal column. The apertures of the aqueductûs vestibuli in the Rays are not situated in a median depression such as is observable in the Dogfish and in all the Sharks. The articular surface in the auditory

region for the hyo-mandibular is sometimes borne on a projecting process, sometimes on the general level of the lateral surface. Sometimes in the Rays there is a smaller articulation behind for the first branchial arch.

The upper and lower jaws—the *palato-quadrate* and *Meckel's cartilage*—are connected with the skull through the intermediation of a *hyo-mandibular* cartilage (Fig. 768, *hy. mn.*; Fig. 788, *h. m.*). In the Sharks the palato-quadrate has a process (absent in the Rays) for articulation with the base of the skull. In Hexanchus and Heptanchus (Fig. 789) there is a prominent post-orbital process of the palato-quadrate for articulation with the post-orbital region of the skull (amphistylic arrangement). At the sides of

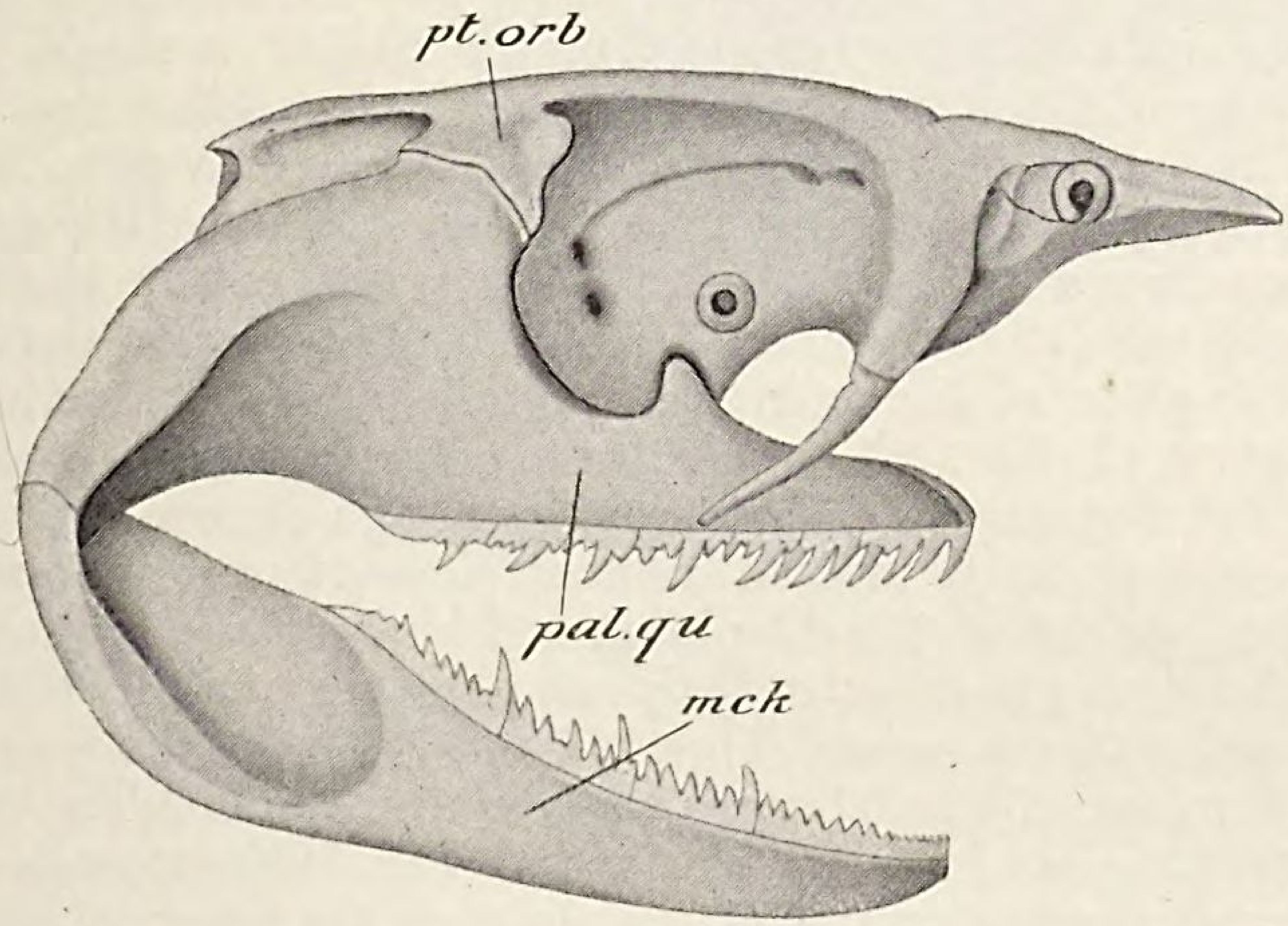


FIG. 789.—Lateral view of the skull of **Heptanchus.** *mck.* Meckel's cartilage; *pal.-qu.* palato quadrate; *pt. orb.* post-orbital process of the cranium, with which the palato-quadrate articulates. (After Gegenbaur.)

the mouth are a series of *labial cartilages*, usually two pairs above and one pair below. Attached to the hyo-mandibular is a thin plate of cartilage—the *spiracular* (Fig. 788, *sp.*)—which supports the anterior wall of the spiracle. The hyoid arch is in most of the Elasmobranchs connected at its dorsal end with the hyo-mandibular, sometimes at its distal extremity, sometimes near its articulation with the skull; but in some Rays it is not so related, but articulates separately and independently with the skull behind the hyo-mandibular, and in the genera *Hypnos* and *Trygonorhina* it articulates with the dorsal portion of the first branchial arch. In the Sharks the hyoid is usually relatively massive; in the Rays it is smaller, and in most cases closely resembles the branchial arches, and bears similar cartilaginous rays; a larger or smaller median element, or basi-hyal, is present in all cases.

There are always five pairs of *branchial arches* except in Hexanchus and Chlamydoselachus, which have six, and Heptanchus, in which there are seven. Their dorsal ends are free in the Sharks, articulated with the anterior vertebral plate of the spinal column in most Rays. Externally they bear a series of slender cartilaginous *branchial rays.* The median ventral elements of the branchial arches are usually more or less reduced, and in some cases are represented by a single *basi-branchial* plate (Fig. 788, *bas. br.*). In the Rays the fifth branchial arch articulates with the pectoral arch, a connection which is absent in the Sharks. A series of slender cartilages—the *extra-branchial cartilages*—absent as such in the Dog-fishes and Rays, support the branchial apertures.

The pectoral arch (Figs. 770, 788, *pect.*) consists of a single cartilage, with, however, in most of the Sharks, a mesial flexible portion by which it is divided into right and left halves. Each lateral half consists of a dorsal, or *scapular*, and a ventral, or *coracoid*, part, the two being separated by the articular surfaces for the basal cartilages of the fin. In the Rays, but not in the Sharks, the dorsal ends of the pectoral arch are connected with the anterior vertebral plate of the spinal column by a distinct articulation, the portion of the arch on which the articular surface is situated sometimes forming an independent cartilage (*supra-scapula*). In *Heptanchus* a small median ventral element may represent the sternal apparatus of the Amphibia and higher Vertebrata.

The *basal pterygiophores* of the pectoral fin are typically three, *pro-*, *meso-*, and *meta-pterygium* (Figs. 770 and 788), but there are sometimes four, and the number may be reduced to two. The pro- and meta-pterygia are in the Rays divided (Fig. 788) into several segments, and the former articulates, through the intermediation of a cartilage termed the *ant-orbital*, with the olfactory region of the skull.

The *pelvic arch* (*pl.*) is usually, like the pectoral, a single cartilage, but in some exceptional cases it consists of two lateral portions. In some cases a median *epipubic process* projects forwards from the pelvic arch, and frequently there is on each side a *præ-pubic* process. A lateral *iliac* process which becomes highly developed in the Holocephali is sometimes represented, and may attain considerable dimensions. The pelvic fin has usually two basal cartilages, representing the pro- and meta-pterygia, but the former is often absent. In the males special cartilages attached to the meta-pterygia support the claspers. With the basal cartilages of both pectoral and pelvic fins are connected a number of jointed cartilaginous fin-rays supporting the expanse of the fin.

The arrangement of the **muscles** is simple. The trunk muscles are divided into a pair of dorsal and a pair of ventral divisions, each composed of many myomeres with intercalated myocommata (Fig. 714, p. 63), following a metameric arrangement. The ventral part, where it forms the muscle of the wall of the abdominal cavity,

is composed externally of obliquely running fibres, and represents one of the two *oblique* muscles of the abdomen of higher forms. Mesially this passes into a median band of longitudinally running fibres corresponding to a primitive *rectus*. The muscles of the limbs are distinguishable into two main sets—those inserted into the limb arch and those inserted into the free part of the appendage. The latter, according to their insertion, act as elevators, depressors, and adductors. A series of circular muscles pass between the cartilages of the visceral arches, and when they contract have the effect of contracting the pharynx and constricting the apertures. A set of muscles pass between the various arches and act so as to approximate them; and a broad sheet of longitudinal fibres divided into myomeres extends forwards from the shoulder girdle to the visceral arches.

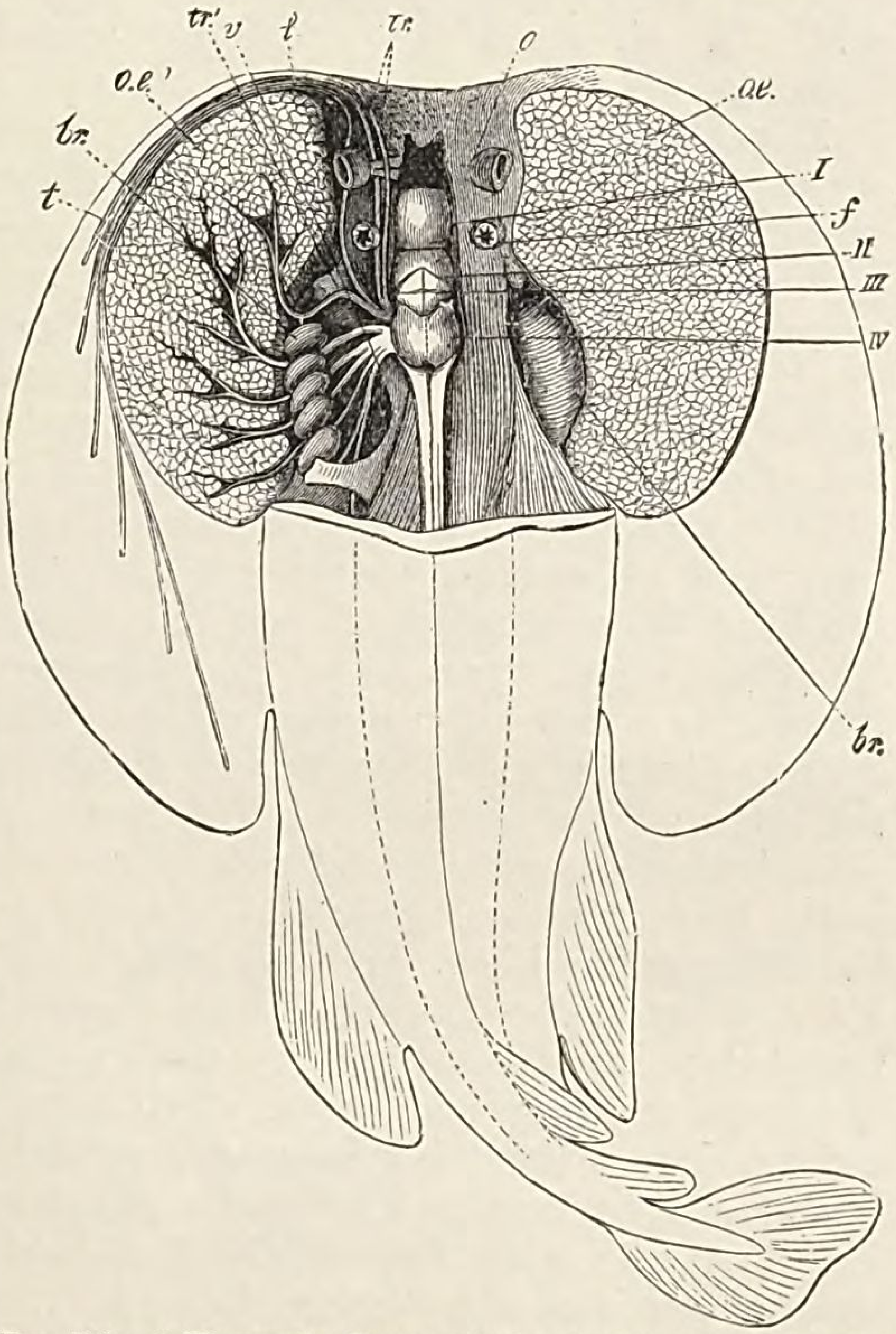


FIG. 790.—A **Torpedo-Ray** with the electric organs dissected out. On the right the surface only of the electric organ (*oe*) is shown. On the left the nerves passing to the organ are dissected out. The roof of the skull is removed to bring the brain into view. *br.* branchiæ; *f*, spiracle; *o*, eyes; *tr.* trigeminal; *tr'*, its electric branch; *v.* vagus; *I*, fore-brain; *II*, mid-brain; *III*, cerebellum; *IV*, electric lobe. (From Gegenbaur.)

Electric organs—organs in which electricity is formed and stored up, to be discharged at the will of the Fish—occur in several Elasmobranchs. They are best developed in the Electric Rays (*Torpedo* and *Hypnos*) (Fig. 790) in which they form a pair of large masses running through the entire thickness of the body, between the head and the margin of the pectoral fin. A network of strands of fibrous tissue forms the support for a number of vertical prisms, each divided by transverse partitions into a large number of compartments or cells. Numerous nerve-fibres pass to the various parts of the organ. These are derived mainly from four nerves,

which originate from an *electric lobe* of the medulla oblongata, with a branch from the trigeminal. By means of the electric shocks which they are able to administer at will to animals in their immediate neighbourhood, the Torpedo-Rays are able to ward off the attacks of enemies and to kill or paralyse their prey. In the other Rays in which the electric organs are developed, they are comparatively small organs situated at the sides of the root of the tail. In all cases the cells are formed from metamorphosed muscular fibres.

Digestive System.—*Teeth* are developed on the palato-quadrate and on Meckel's cartilage. They are arranged in several parallel rows, and are developed from a groove at the back of the jaw, successive rows coming to the front, and, as they become worn out, falling off and becoming replaced by others. In the Sharks the teeth are usually large and may be long, narrow, and pointed, or triangular with serrated edges, or made up of several sharp cusps; in the Rays, however, the teeth are more or less obtuse, sometimes, as in the Eagle-Rays, forming a continuous pavement of smooth plates covered with enamel, adapted to crushing food consisting of such objects as Shell-fish and the like. The Sharks have a prominent tongue supported by the median basi-hyal; this is entirely or almost entirely absent in the Rays. There are no salivary glands. The various divisions of the enteric canal are similar in all the members of the class to what has already been described in the case of the Dog-fish. A spiral valve is always present in the large intestine, though its arrangement varies considerably in the different families. In some cases (e.g. *Carcharias*) the fold is not a spiral one, but, attached by one edge in a nearly longitudinal line to the intestinal wall, is rolled up in the shape of a scroll. A cœcum occurs in Læmargus. The rectum always terminates in a *cloaca*, into which the urinary and genital ducts also lead. There is always a voluminous liver and a well-developed pancreas.

A *thyroid* lies in the middle line behind the lower jaw. A representative of the *thymus* lies on either side, a little below the upper angles of the branchial clefts.

The **respiratory organs** of the Elasmobranchii always have the general structure and arrangement already described in the case of the Dog-fish.

In addition to the gills supported on the hyoid and branchial arches there is also in the Notidanidæ a gill in the spiracular cleft —the *spiracular gill*—represented in many others by a *rete mirabile* or network of blood-vessels. In Selache (the Basking Shark) there are a series of slender rods, the *gill-rakers*, which impede the passage outwards through the branchial clefts of the small animals on which those Sharks feed.

Blood System.—The *heart* has in all essential respects the same structure throughout the group. The conus arteriosus is

always contractile, and contains several rows of valves. The general course of the circulation is the same in all (see p. 145), with some variation in the precise arrangement of the vessels. In some of the Rays the ventral aorta and the roots of the afferent vessels are partly enclosed in the cartilage of the basi-branchial plate.

The **brain** attains a much higher stage of development than in the Cyclostomata. The fore-brain greatly exceeds the other divisions in size. In Scymnus there are two widely-separated parencephalic lobes or *cerebral hemispheres* containing large lateral ventricles. In other genera there is at most, as in the Dog-fish, a median depression of greater or less depth, indicating a division into two lateral portions. In Scyllium, as already pointed out, there is a median prosocœle which gives rise anteriorly to two lateral ventricles, or paracœles, and the same holds good of Rhina and Acanthias. In the Rays there is only a very small prosocœle without anterior prolongations. The olfactory lobes are of great size, with in some cases short and thick, in others longer and narrower, stalks. In Scyllium, Rhina, and Acanthias, as well as in Scymnus, they contain ventricles; in the Rays they are solid.

The *diencephalon* is of moderate extent. On its lower aspect are a pair of rounded *lobi inferiores*, which are of thenature of a bilobed dilated *infundibulum*, and a median *saccus infundibuli* and *saccus vasculosus*, both diverticula of the infundibulum; directly behind the saccus vasculosus lies the hypophysis. The *epiphysis* is long and narrow.

In the hind-brain the *cerebellum* is relatively greatly elongated, and overlaps the optic lobes and sometimes also the diencephalon in front. Behind it extends over the anterior part of the *medulla oblongata*. It usually contains a cerebellar ventricle or *epicœle*. The medulla is elongated in the Sharks, shorter and more triangular in the Rays. The Electric Rays are characterised by the presence of the *electric lobes*, rounded elevations of the floor of the fourth ventricle.

Organs of Sense.—The *sense-organs of the integument* are almost always simple or enclosed in branched canals, the *mucous* or *sensory canals*, and are supplied by the lateral branch of the vagus and by branches of the trigeminal, facial, and glosso-pharyngeal. On the head and anterior trunk region larger or smaller canals occur having a number of dilatations—the *ampullæ*, filled with gelatinous matter given off from them; in these are nerve-endings. Some Sharks are exceptional in the presence of an open groove for the lodgment of the integumentary sense-organs.

The *olfactory organs* are a pair of cavities opening on the lower surface of the head, a little distance in front of the mouth, and enclosed by the cartilaginous olfactory capsules of the skull.

Their inner surface is raised up into a number of ridges on which the fibres of the olfactory nerves are distributed. The *eye* has a cartilaginous sclerotic and is in most cases attached to the inner wall of the orbit by means of a cartilaginous stalk. A fold of the conjunctiva corresponding to the *nictitating membrane*, or third eyelid of higher Vertebrates, occurs in some Sharks. The *ear* consists of the three semicircular canals with their ampullæ; of the membranous vestibule, which is partly divided into two; and of a canal—the *aqueductus vestibuli* or *endolymphatic duct*—which opens on the exterior on the dorsal surface of the head. In the Rays the semicircular canals form almost complete circles and open separately into the vestibule by narrow ducts.

Urino-genital Organs.—The *kidneys*, as already noticed in the account given of the Dog-fish, differ somewhat in their relations in the two sexes. In the male the anterior portion persists as the epididymis, and its duct becomes the spermiduct, while the posterior portion, which is the functional kidney, has a duct, the *ureter*, of its own. In the female there is no direct connection between the reproductive and renal organs; the anterior portion of the kidney may be functional, and its duct persists, opening along with those of the posterior portion. In the male the ureters open into a median chamber—the *urino-genital sinus*—a special compartment of the cloaca, which receives also the spermiducts: this communicates with the general cavity of the cloaca by a median opening situated on a papilla—the *urino-genital* papilla. In the female there is a median *urinary sinus*, into which the ureters open, or the latter open separately into the cloaca.

Save in certain exceptional cases (*e.g.* the Dog-fish), there are two ovaries, varying considerably in form, but always characterised towards the breeding season by the great size of the Graafian follicles enclosing the mature ova. The oviducts (Müllerian ducts) are quite separate from the ovaries. The right and left oviducts come into close relationship anteriorly, being united in the middle on the ventral surface of the œsophagus, where each opens by a wide orifice into the abdominal cavity, or both open by a single median aperture. The following part of the oviduct is very narrow; at one point it exhibits a thickening, due to the presence in its walls of the follicles of the *shell-gland*. Behind this is a dilated portion which acts as a *uterus*; and this communicates with the cloaca through a wide *vagina*. A considerable number of the Elasmobranchii are viviparous, and in these the inner surface of the uterus is beset with numerous vascular villi, while the shell-gland is small or vestigial.

The testes are oval or elongate: the convoluted epididymis is connected with the anterior end by efferent ducts, and passes posteriorly into the vas deferens. The latter is dilated near its

opening into the urino-genital sinus to form an ovoid sac—the *vesicula seminalis*. A large thin-walled *sperm-sac* is sometimes present, opening close to the aperture of the vas deferens. The Müllerian ducts are vestigial in the male.

Impregnation is internal in all the Elasmobranchs with the exception of Læmargus (the Greenland Shark), the claspers acting as intromittent organs by whose agency the semen is transmitted into the interior of the oviducts.

In all the Elasmobranchs the ova are very large, consisting of a large mass of yolk-spherules held together by means of a network of protoplasmic threads, with, on one side, a disc of protoplasm—the *germinal disc*. The process of maturation is similar to that observable in holoblastic ova; one polar globule is thrown off in the ovary, the other apparently at impregnation. The ripe ovum ruptures the wall of the enclosing follicle and so passes into the abdominal cavity to enter one of the oviducts through the wide abdominal opening. Impregnation takes place in the oviduct, and the impregnated ovum in the oviparous forms becomes surrounded by a layer of semi-fluid albumen and enclosed in a chitinous shell secreted by the shell-gland. The shell varies in shape somewhat in the different groups: most commonly, as in the Dogfishes (Fig. 780), it is four-cornered, with twisted filamentous appendages at the angles, by means of which it becomes attached to sea-weeds and the like. In the Skates the filaments are absent. In the Port Jackson Sharks (Cestracion) (Fig. 791) it is an ovoid body, the wall of which presents a broad spiral flange. Enclosed in the shell, the young Elasmobranch goes through its development until it is fully formed, when it escapes by rupturing the egg-shell. In the viviparous forms the ovum undergoes its development in the uterus, in which for the most part it lies free, except in some *Mustelidæ*, in which there is a close connection between the yolk-sac of the fœtus and the wall of the uterus, folds of the former interdigitating with folds of the latter, and nourishment being thus conveyed from the vascular system of the mother

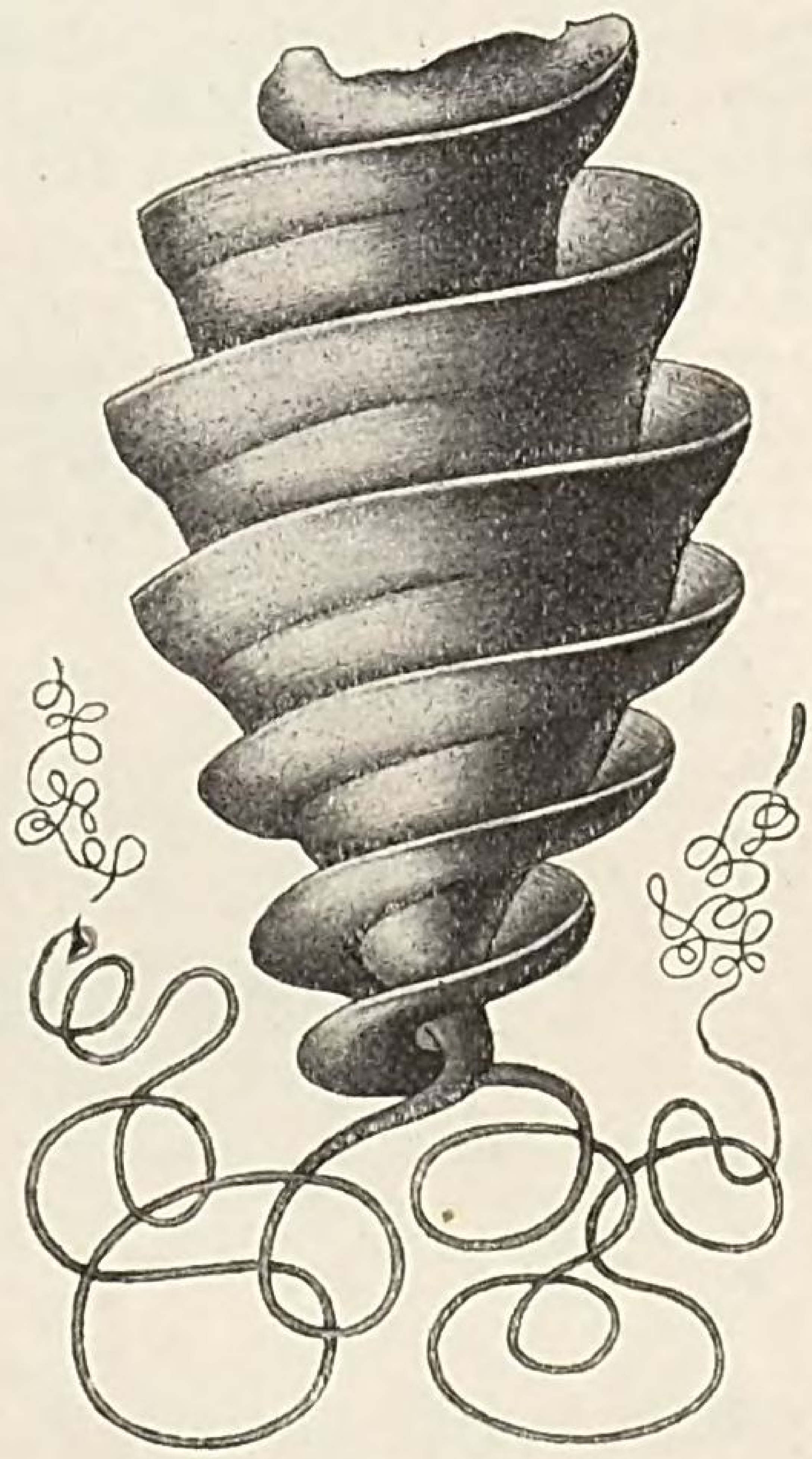


FIG. 791.—Egg-case of **Cestracion galeatus.** (After Waite.)

to that of the fœtus. In *Mustelus antarcticus* the uterus is divided by septa into several compartments, each containing a single fœtus. In some of the viviparous forms a distinct, though very delicate, shell, sometimes having rudiments of the filaments, is formed, and is thrown off in the uterus. In the genera Rhinobatus and Trygonorhina, which are both viviparous, each shell encloses, not one egg, but three or four. Læmargus appears to differ from all the rest of the Elasmobranchii in having the ova fertilised after they have been deposited as well as in the small size of the ova.

Development.—Segmentation is meroblastic, being confined to the germinal disc, which, before dividing, exhibits amœboid movements. While segmentation is going on in the germinal disc there appear a number of nuclei, the source of which is not certain, in the substance of the yolk. When segmentation is complete the blastoderm appears as a lens-shaped disc, thicker at one end—the embryonic end. It is found to consist of two layers of cells,—an upper layer in a single stratum, and a lower layer several cells deep. A segmentation-cavity appears early among the cells of the lower layer; the lower-layer cells afterwards disappear from the floor of this, the cavity then coming to rest directly on the yolk.

An in-folding of the blastoderm (Fig. 792) now begins at the thickened embryonic edge of the blastoderm, which here becomes

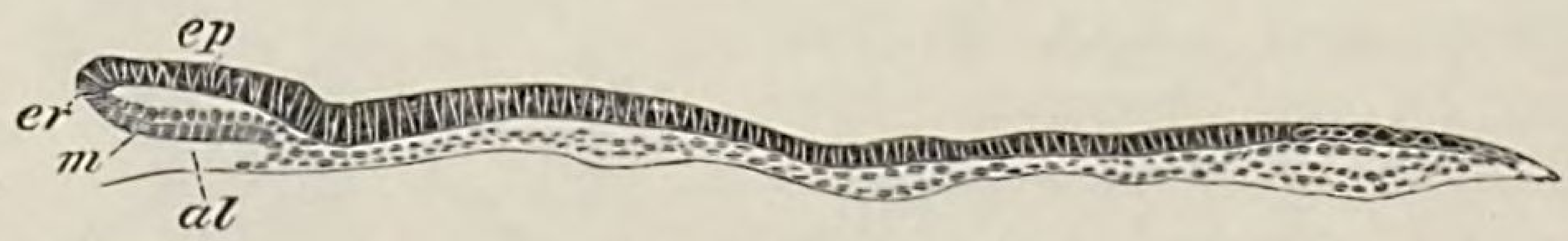


FIG. 792.—Longitudinal section through the blastoderm of a **Pristiurus** embryo before the medullary groove has become formed, showing the beginning of the process of infolding or invagination. *al.* archenteron; *ep.* ectoderm; *er.* embryonic rim; *m.* mesoderm. (From Balfour.)

continuous with the cells of the lower layer. The cavity (*al*), at first very small, formed below this in-folding is the rudiment of the *archenteron*, and the cells lining this cavity above, which form a definite layer, partly derived from the in-folded ectoderm, partly from the cells of the lower layer, are the beginning of the definite *endoderm*. The edge of the in-folding, entitled the *embryonic rim*, is obviously the equivalent of the dorsal lip of the blastopore in Amphioxus. The endoderm and its underlying cavity soon grow forwards towards the segmentation cavity. Under the latter appears a floor of lower-layer cells, but the cavity soon becomes obliterated as the archenteron develops.

After the formation of the embryonic rim a shield-like *embryonic area* is distinguishable in front of it, with two folds bounding a groove—the *medullary groove*. The mesoderm becomes established at about the same time. It is formed from the lower-

layer cells and assumes the form of a pair of independent plates —one on either side of the middle line of the body.

As the blastoderm extends over the yolk the edge forms a ridge continuous with the embryonic rim. The latter assumes the form of two prominent *caudal swellings* (Fig. 794, *cd.*). The medullary groove meanwhile deepens, and its edges grow over, as in Amphioxus and the Urochorda, so as to form a canal (Fig. 793, *C*; Fig. 795). The union takes place first in the middle, the anterior

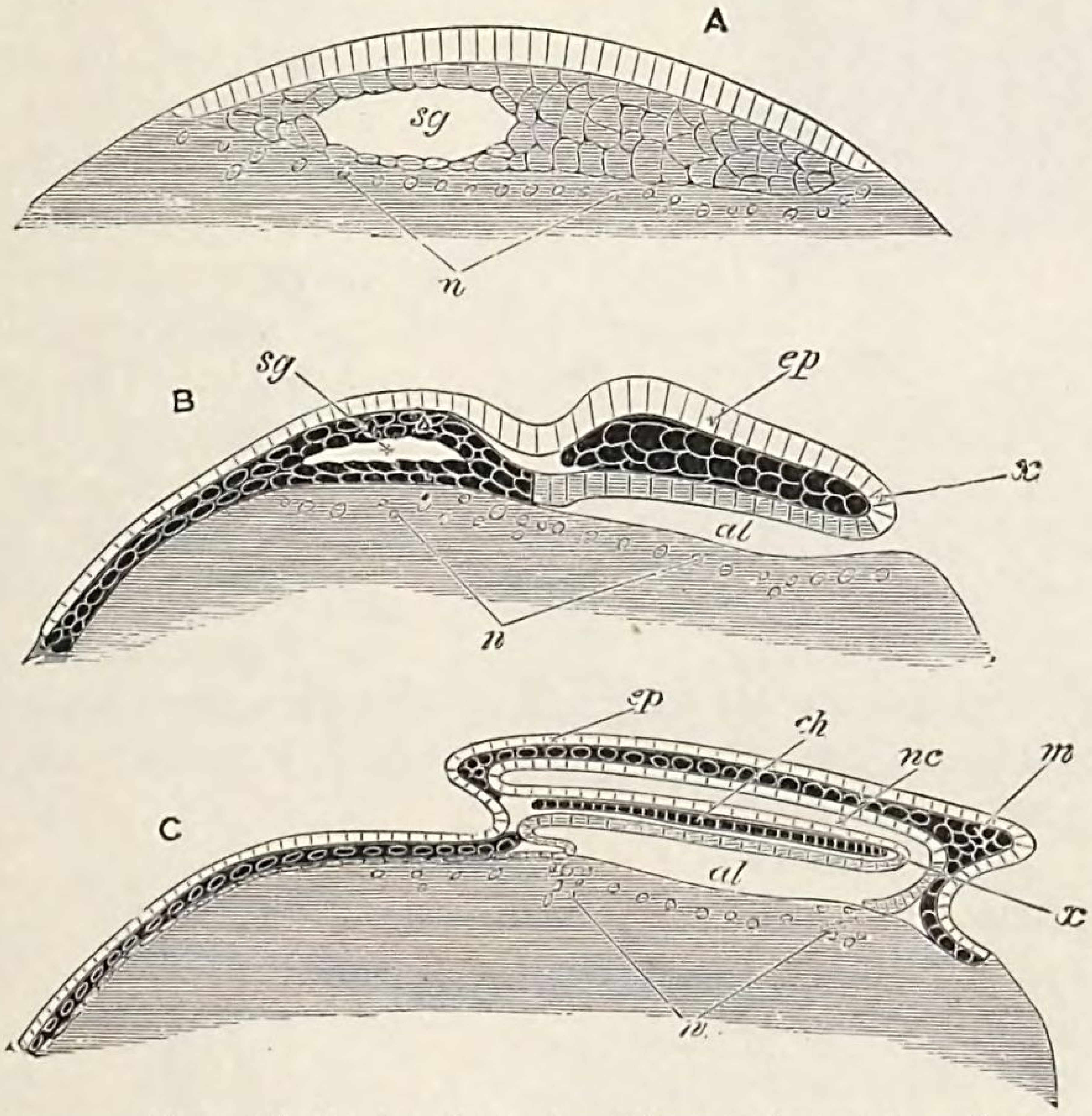


FIG. 793.—Diagrammatic longitudinal sections of an **Elasmobranch embryo.** *A*, section of the young blastoderm with segmentation-cavity enclosed in the lower layer cells. *B*, older blastoderm with embryo in which endoderm and mesoderm are distinctly formed, and in which the alimentary slit has appeared. The segmentation-cavity is still represented as being present, though by this stage it has in reality disappeared. *C*, older blastoderm with embryo in which the neural canal has become formed and is continuous posteriorly with the alimentary canal. *Ectoderm* without shading; *mesoderm* and also *notochord* black with clear outlines to the cells; endoderm and lower layer cells with simple shading. *al.* alimentary cavity; *ch.* notochord; *ep*, ectoderm; *m.* mesoderm; *n.* nuclei of yolk; *nc.* neurocœle; *sg.* segmentation-cavity; *x.* point where ectoderm and endoderm become continuous at the posterior end of the embryo. (From Balfour.)

and posterior parts (Fig. 795, *neur.*) remaining open for a while. When the posterior part closes, it does so in such a way that it encloses the blastopore, and there is thus formed, as in the Ascidian, a temporary passage of communication between the medullary canal and the archenteron—the *neurenteric passage*.

The ectoderm gives rise, as in Vertebrates in general, not only to the epidermis and the central nervous system, but also to the peripheral nervous system, the lining membrane of the olfactory sacs, the lens of the eye, and the lining membrane of the auditory labyrinth, of the mouth and gill clefts, and of the cloaca.

The notochord (Fig. 793, *ch.*) is developed as a cord of cells derived from the lower layer.

Each of the two plates of mesoderm soon divides into two layers, *somatic* and *splanchnic*, with a cavity between them. The inner part of each separates off from the rest and becomes divided by transverse fissures into a series of squarish masses, the *proto-vertebræ*, the outer part forming a broad plate, the *lateral plate*. The splanchnic layer of the proto-vertebræ sends off cells round the notochord to form the bodies of the vertebræ, the remainder giving rise to the muscles of the voluntary system. The isthmus between the lateral plate and the protovertebræ, containing a prolongation of the cavity, gives rise to the pronephric duct and tubules. The lateral plates eventually unite ventrally, and their cavities coalesce to form the body cavity. The parts derived from the mesoderm are the system of voluntary muscles, the dermis, the inter-muscular connective tissue, the endoskeleton, the muscular and connective-tissue layers of the alimentary canal, the vascular system,[1] and the generative organs. The segmentation of the mesoderm does not at first extend into the

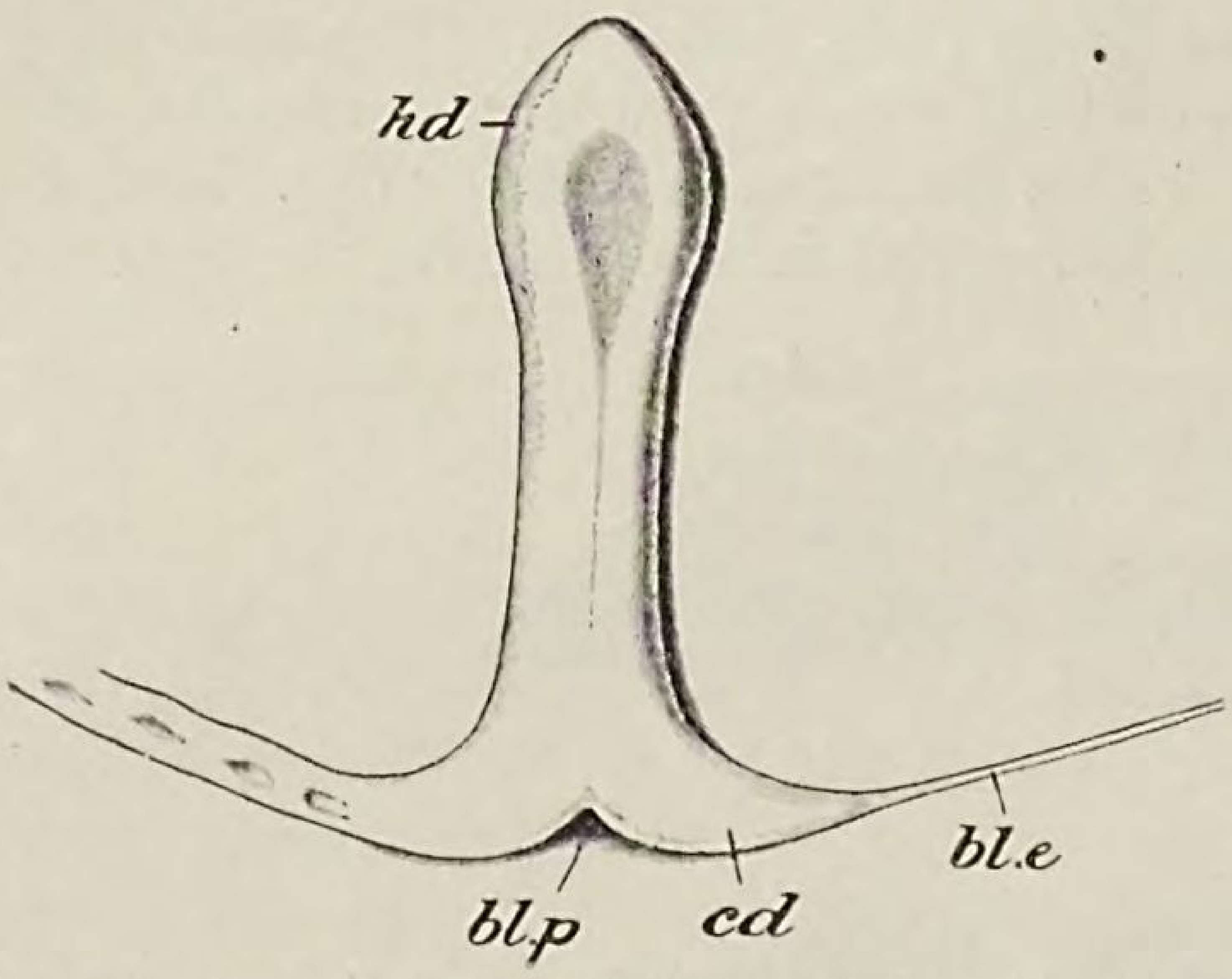


FIG. 794.—Embryo of **Scyllium canicula** with the tail-swellings well marked and the medullary groove just beginning. *bl. e.* edge of blastoderm; *bl. p.* blastopore; *cd.* caudal swellings; *hd.* head. (After Sedgwick.)

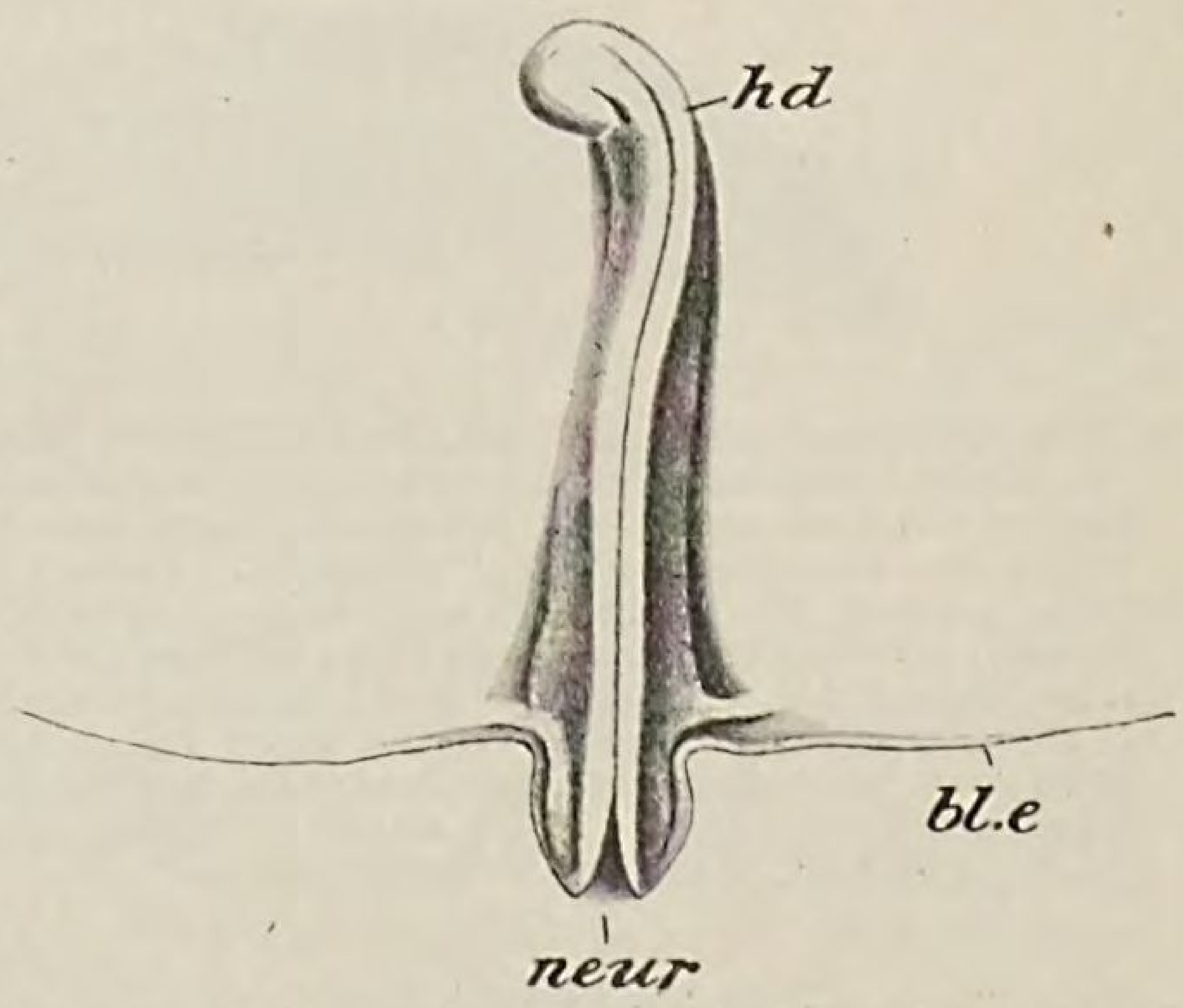


FIG. 795.—Embryo of a **Ray** with the medullary groove closed except at the hind end. The notched embryonic part of the blastoderm has grown faster than the rest and come to project over the surface of the yolk. *bl. e.* edge of blastoderm; *hd.* head; *neur.* unenclosed part of the neurocœle. (After Sedgwick.)

[1] There is some uncertainty as to the germinal layer from which the internal lining membrane of the heart and blood-vessels is derived. In *Acanthias vulgaris*, if not in others, it seems to be derived from the endoderm, and the entire vascular system is to be looked upon as a separated-off part of the archenteron.

head, but, on the formation of the gill-clefts, a series of mesodermal segments appear, the cells of which give rise to the muscles of the branchial, hyoid, and mandibular arches, and probably also of the palato-quadrate and the eye.

By degrees the body of the young fish becomes moulded on the blastoderm. This is effected by the formation of a system of folds, anterior, posterior, and lateral, which grow inwards in such a way as to separate off the body of the embryo from the rest of the blastoderm enclosing the yolk. As the folds approach one another in the middle, underneath the embryo, they come to form a constriction connecting the body of the embryo with the yolk enclosed in the extra-embryonic part of the blastoderm. The process may be imitated if we pinch off a portion of a ball of clay, leaving only a narrow neck connecting the pinched-off portion with the rest. The body of the embryo thus becomes folded off from the *yolk-sac* and comes to be connected with it only by a narrow neck or yolk-stalk (Fig. 796).

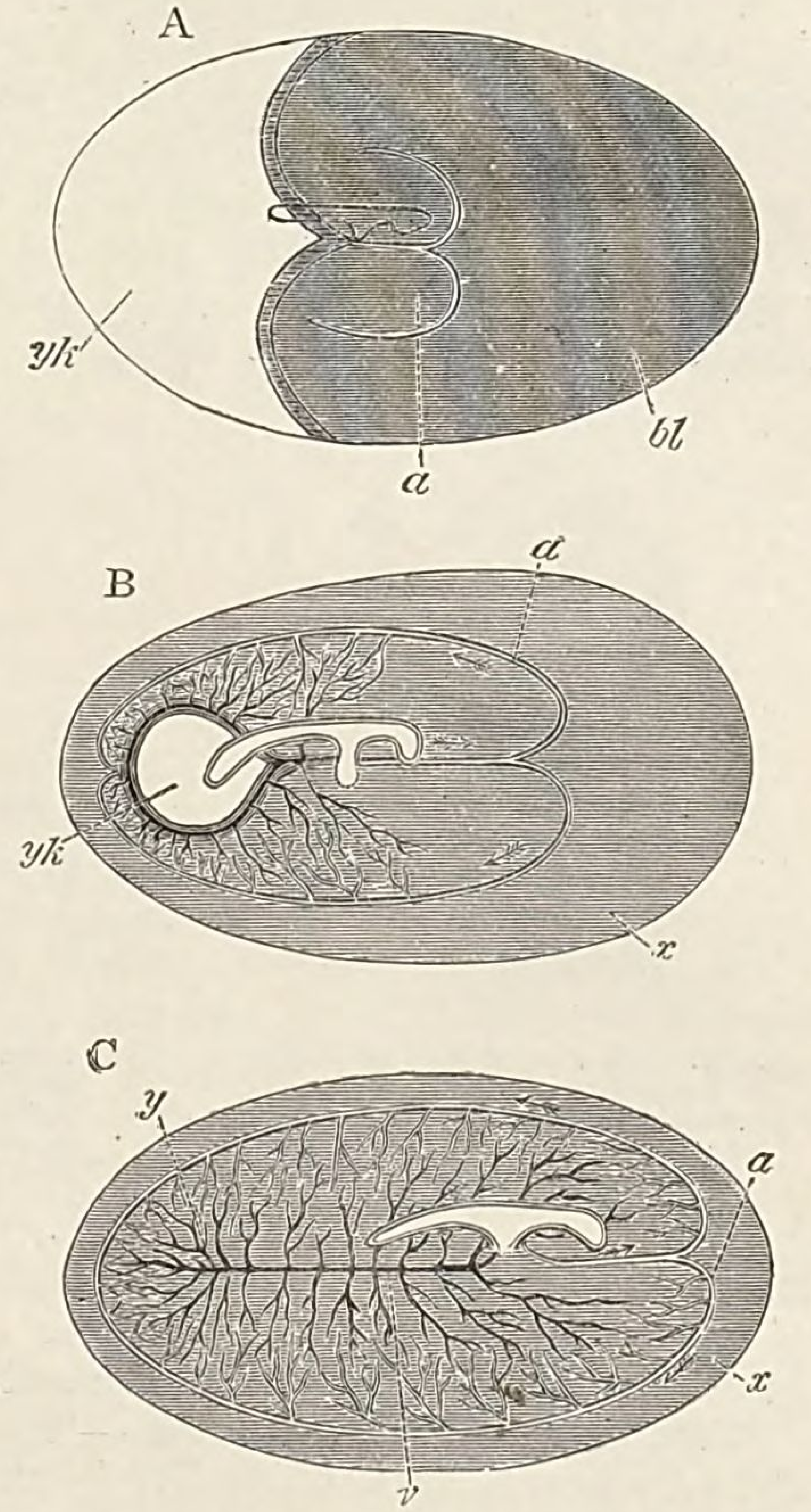


FIG. 796.—Three views of the developing egg of an **Elasmobranch**, showing the embryo, the blastoderm, and the vessels of the yolk-sac. The shaded part (*bl.*) is the blastoderm, the white part the uncovered yolk. *A*, young stage with the embryo still attached at the edge of the blastoderm. *B*, older stage with the yolk not quite enclosed by the blastoderm. *C*, stage after the complete closure of the yolk. *a.* arterial trunks of yolk-sac; *bl.* blastoderm; *v.* venous trunks of yolk-sac; *y*, point of closure of the yolk blastopore; *x*, portion of the blastoderm outside the arterial sinus terminalis. (From Balfour.)

The head and tail of the young Fish soon become differentiated, and a series of involutions at the sides of the neck (Fig. 797) form the branchial clefts and spiracle. A number of very delicate long filaments (Fig. 797) grow out from these apertures; these are the provisional gills, which atrophy as the development

approaches completion, their bases alone persisting, to give rise to the permanent gills. The great development of these gill-filaments in the embryos of some viviparous forms suggests that in addition to their respiratory functions they may also serve as organs for the absorption of nutrient fluids secreted by the villi of the uterine wall.[1] The fins, both paired and unpaired, appear as longitudinal ridges of the ectoderm enclosing mesoderm. In some Elasmobranchs the paired fins are at first represented on each side by a continuous ridge or fold, which only subsequently becomes divided into anterior and posterior portions—the rudiments respectively of the pectoral and pelvic fins. Into these folds penetrate a series of buds from the protovertebræ; these, the

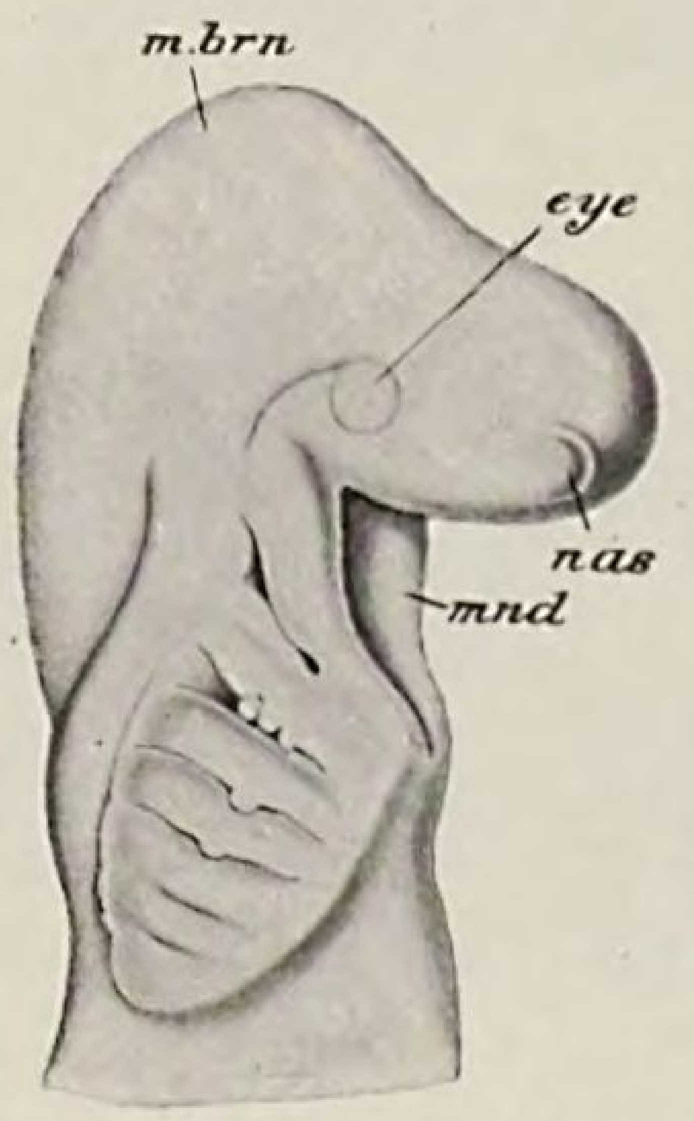


FIG. 797.—Side view of head of embryo of **Scyllium canicula,** with the rudiments of the gills on the first and second branchial arches. *eye*, eye; *m. brn.* mid-brain; *mnd.* mandible; *nas.* nasal sac. (After Sedgwick.)

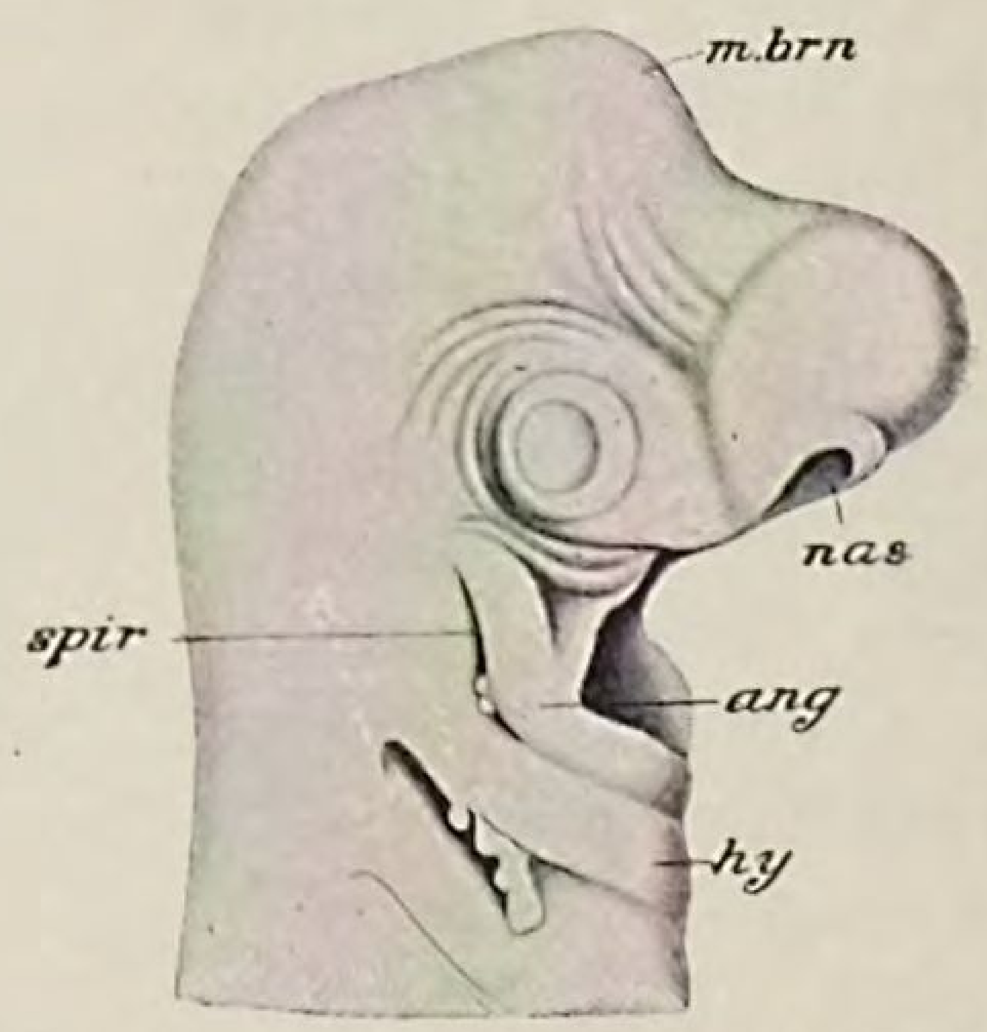


FIG. 798.—Side view of the head of **Scyllium canicula** at a somewhat later stage. The gills have increased in number and are present on the mandibular arch. *ang.* angle of the jaw; *hy.* hyoid; *m. brn.* mid-brain; *nas.* nasal sac; *spir.* spiracle. (After Sedgwick.)

muscle-buds, give rise to the fin-muscles; at first, from their mode of origin, they present a metameric arrangement, but this is in great measure lost during development.

Ethology and Distribution.—The habits of the active, fierce, and voracious Sharks, which live in the surface-waters of the sea, making war on all and sundry, contrast strongly with those of the more sluggish Rays, which live habitually on the bottom, usually in shallow water, and feed chiefly on Crustaceans and Molluscs, with the addition of such small Fishes as they can capture. As a group, the Elasmobranchs, more particularly the Sharks, are distinguished by their muscular strength, the activity of their movements, and also by the acuteness of their senses of sight and smell.

The only deep-water Elasmobranch known is a species of Ray, which extends to a depth of over 600 fathoms.

[1] In a species of Trygon the nutrient secretion is stated to pass into the enteric canal through the spiracles.

None of the Elasmobranchs are of very small size, and comprised among them are the largest of living Fishes. The harmless Basking Sharks (*Selache*) sometimes attain a length of 35 feet or more, the formidable Great Blue Shark (*Carcharodon*) sometimes reaches 40 feet, and some of the Rays also attain colossal dimensions. In this respect, however, recent Sharks and Rays are far behind some of the fossil forms, some of which, if their general dimensions were in proportion to the size of their teeth, must have attained a length of as much as sixty feet.

The earliest fossil remains of Elasmobranch Fishes that have been found occur in rocks belonging to the Upper Silurian period. Throughout the Palæozoic Epoch the Elasmobranchs constituted a very important section of the fauna—a large proportion of the fish-remains that have been found in palæozoic formations being the remains of Elasmobranchs, mainly in the form of spines and teeth. Most of the palæozoic Elasmobranchs were characterised by a great development of the exoskeleton. The teeth differ from those of existing forms in being provided with broad bases by means of which they articulated together, and in various groups there is a union of the teeth by the coalescence of their bases so as to form broad crushing plates. A similar union is not uncommon between the parts of the general exoskeleton, a good many palæozoic Sharks having been encased in an armour of solid plates formed by such a coalescence. In the endoskeleton there is to be observed among the fossil Elasmobranchs a gradual advance in the degree of calcification of the spinal column from the palæozoic forms onwards, the Protoselachii alone among existing forms representing in this respect the condition which seems to have prevailed in the most ancient members of the class.

The group (Cestracionts) now represented by two or three species of Port Jackson Sharks seems to have been very abundant in palæozoic times.

The extinct Pleuracanthea, together with Cladoselachus, which, as briefly stated in the sketch of the classification, differ from the other known members of the class in the structure of the fins and other points, range from the Devonian to the Permian, and are perhaps also represented in the Trias.

Sub-Class II.—Holocephali.

The existing representatives of the Holocephali are included under the single family *Chimæridæ*, containing three genera—*Chimæra*, *Callorhynchus*, and *Harriotta*. Even taking in fossil forms, the group is a very small one; it agrees in many fundamental characteristics with the Elasmobranchii, but presents so many important differences that it cannot well be included in that sub-class. Of the recent genera, Chimæra, the so-called

" King of the Herrings " (Fig. 799, *A*) is found on the coasts of Europe and Japan, the west coast of North America, and at the Cape of Good Hope; Callorhynchus (*B*) is tolerably abundant in the South Temperate seas; Harriotta is a deep-sea form.

External Characters.—The general form of the body is Shark-like, but the large, compressed head and small mouth are strikingly different from the depressed, shovel-shaped head and wide mouth of most Selachians. The mouth is bounded by lip-like folds, two of

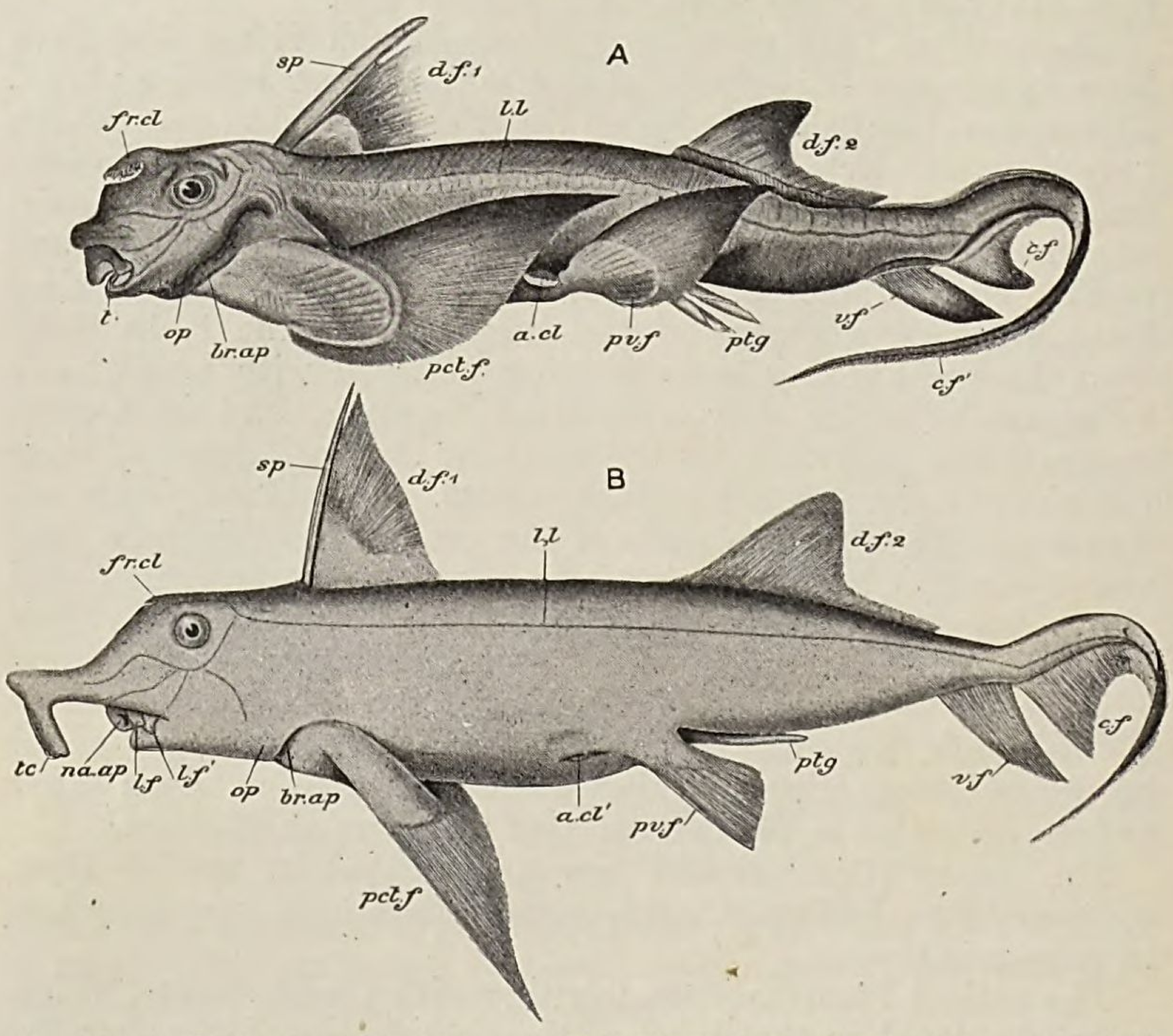


FIG. 799.—A, **Chimæra monstrosa;** B, **Callorhynchus antarcticus**. *a. cl.* anterior clasper; *a. cl.'* pouch for its reception; *br. ap.* branchial aperture; *c. f.* caudal fin; *c. f.'* its whip-like prolongation; *d. f. 1, d. f. 2,* dorsal fins; *fr. cl.* frontal clasper; *l. f., l. f.'* labial folds; *l. l.* lateral line; *na. ap.* nasal aperture; *op.* operculum; *pct. f.* pectoral fin; *ptg.* pterygopodia; *pv. f.* pelvic fin; *t.* teeth; *tc.* tactile flap; *v. f.* ventral fin. (A, after Cuvier.)

which (*B*, *l.f.*, *l.f.'*), placed laterally and supported by labial cartilages, resemble the folds in which the premaxillæ and maxillæ of Bony Fishes are enclosed: a third fold, external to and concentric with the mandible, is also supported by labial cartilages and has the appearance of a second or external lower jaw. In Chimæra the snout is blunt, in Harriotta long and pointed; in Callorhynchus it is produced into a rostrum, from the end of which depends a large cutaneous flap (*B*, *tc*) abundantly supplied with nerves and evidently serving as an important tactile organ.

A still more important difference from Elasmobranchs is the possession of only a single external branchial aperture (*br. ap.*), owing to the fact that a fold of skin, the *operculum* (*op.*), extends backwards from the region of the hyoid arch and covers the true gill-slits, which thus come to open into a common chamber situated beneath the operculum and communicating with the exterior by a single secondary branchial aperture placed just anterior to the shoulder-girdle. Equally characteristic is the circumstance that the urino-genital aperture is distinct from and behind the anus, there being no cloaca.

There are two large dorsal fins (*d.f. 1*, *d.f. 2*) and a small ventral (*v. f.*); the caudal fin (*c. f.*) is of the ordinary heterocercal type in the adult Callorhynchus, but in the young (Fig. 805) the extremity of the tail proper is not upturned, and the fin-rays are arranged symmetrically above and below it, producing the form of tail-fin called *diphycercal*. In Chimæra the dorsal lobe of the tail may be produced into a long whip-like filament (*c. f'*.). The pectoral (*pct. f.*) and pelvic (*pv. f.*) fins are both large, especially the former.

In the male there is a horizontal slit (*B, a. cl.'*) situated a little in front of the pelvic fins; it leads into a shallow glandular pouch, from which can be protruded a peculiar and indeed unique apparatus, the *anterior clasper* (*A, a. cl.*), consisting of a plate covered with recurved dermal teeth, to which is added, in Callorhynchus, a plate rolled upon itself to form an incomplete tube. The use of this apparatus is not known; as it lies in the line of the hypothetical continuous lateral fin, and as the cartilages which support it articulate with the pelvic girdle, it seems possible that it may have arisen as a portion of the lateral fin, which has atrophied in all other Craniata. If this be so, it must be looked upon as a third or intermediate paired appendage. A rudiment of the pouch occurs in the female, although the clasper itself is absent. The male possesses, in addition, a pair of the ordinary *pterygopodia* or posterior claspers (*ptg.*) and is further distinguished by the presence of a little knocker-like structure, the *frontal clasper* (*fr. cl.*), on the dorsal surface of the head. In Harriotta the claspers are poorly developed, and the frontal clasper is absent.

The lateral line (*l. l.*) is an open groove, and there are numerous sensory pits, arranged in curved lines, on the head. The skin is smooth and silvery, and bears for the most part no exoskeletal structures. There are, however, delicate, recurved dermal teeth on the anterior and frontal claspers, and the first dorsal fin is supported by an immense bony spine or *dermal defence* (*sp.*). In the young, moreover, there is a double row of small dermal teeth along the back.

Endoskeleton.—The *vertebral column* consists of a persistent

notochord with cartilaginous arches. In Chimæra there are calcified rings (Fig. 800, *c. r.*) embedded in the sheath of the notochord. The anterior neural arches are fused to form a high, compressed, vertical plate, to which the first dorsal fin is articulated. The *cranium* (Figs. 801 and 802) has a very characteristic form, largely owing to the compression of the region between and in front of the large orbits, which are separated from the cranial cavity by membrane only in Callorhynchus (Fig. 802, *or.*); in Chimæra they lie above the level of the cranial cavity and are separated from one another by a median vertical partition of fibrous tissue (Fig. 801, *i. o. s*). At first sight the palato-quadrate, or primary upper jaw, appears to be absent, but a little consideration shows it to be represented by a triangular plate (*pal. qu.*) which extends downwards and outwards from each side of the cranium and presents at its apex a facet for the articulation of the mandible. The palato-quadrate is therefore fused with the cranium and furnishes the sole support for the lower jaw; in a word, the skull is *autostylic*. The pituitary fossa (Fig. 802, *s. t.*) is very deep and inclined backwards; on the ventral surface of the basis cranii is a pit (*pt.*) for the extra-cranial

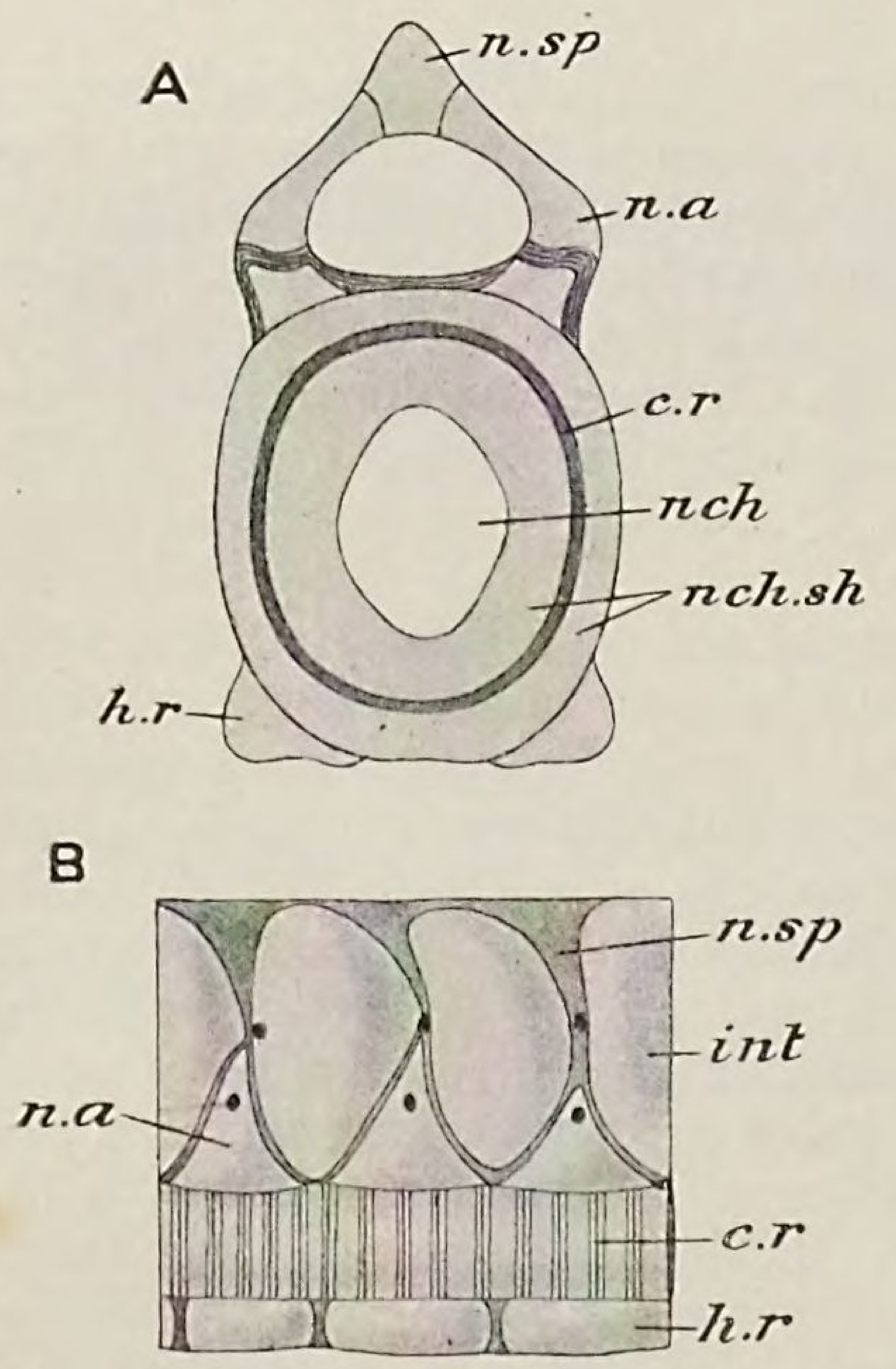


FIG. 800.—**Chimæra monstrosa.** A, transverse section of vertebral column; B, lateral view of the same. *c. r.* calcified ring; *h. r.* hæmal ridge; *int.* intercalary piece; *n. a.* neural arch; *nch.* position of notochordal tissue; *nch. sh.* sheath of notochord; *n. sp.* neural spine. (After Haasse.)

portion of the pituitary body. The posterior portion of the cranial cavity is very high; the anterior part—containing most of the fore-brain—is low and tunnel-like, and has above it a cavity of almost equal size (*Nv. 5 o'.*) for the ophthalmic branches of the fifth nerves. The greater part of the membranous labyrinth is lodged in a series of pits on the side-walls of the cranium (*a.s.c.*, *p.s.c.*), and is separated from the brain by membrane only. The occipital region articulates with the vertebral column by a single saddle-shaped surface or condyle (*oc. cn.*). There is a great development of labial cartilages, particularly noticeable being a large plate which, in

Callorhynchus, lies just externally to the mandible, nearly equalling it in size and having the appearance of a secondary or external jaw. In Callorhynchus the snout is supported by three cartilaginous rods growing forward from the cranium, of which one (*r*) is median and dorsal and represents the rostrum; these, as well as the great lower labial (Fig. 801, *lb*3.), are represented by comparatively small structures in Chimæra.

The hyoid resembles the branchial arches in form and is little superior to them in size. Above the epihyal (Fig. 801, *e. hy.*) is a small cartilage (*ph. hy.*), evidently serially homologous with the pharyngo-branchials, and therefore to be considered as a *pharyngo-hyal*. It represents the hyo-mandibular of Elasmobranchs, but,

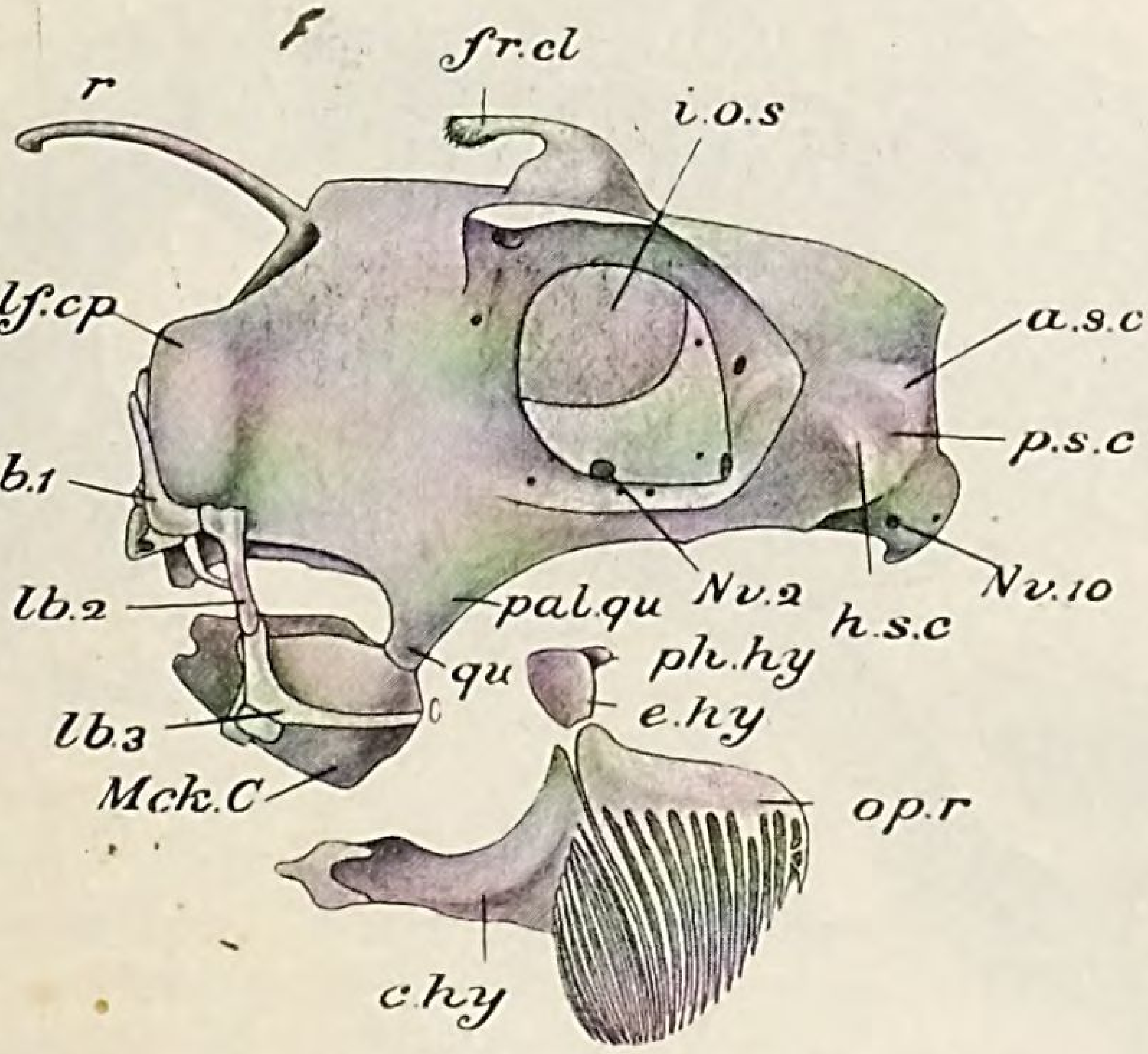


FIG. 801.—**Chimæra monstrosa,** lateral view of skull. *a. s. c.* position of anterior semicircular canal; *c. hy.* cerato-hyal; *e. hy.* epi-hyal; *fr. cl.* frontal clasper; *h. s. c.* position of horizontal semicircular canal; *i. o. s.* inter-orbital septum; *lb. 1*, *lb. 2*, *lb. 3*, labial cartilages; *Mck. c.* mandible; *Nv. 2*, optic foramen; *Nv. 10*, vagus foramen; *olf. cp.* olfactory capsule; *op. r.* opercular rays; *pal. qu.* palato-quadrate; *ph. hy.* pharyngo-hyal; *p. s. c.* position of posterior semicircular canal; *qu.* quadrate region; *r.* rostrum. (After Hubrecht.)

having no function to perform in the support of the jaws, it is no larger than the corresponding segments in the succeeding arches. Long cartilaginous rays (*op. r.*) for the support of the operculum are attached to the cerato-hyal.

The first dorsal fin is remarkable for having all its pterygiophores fused into a single plate, which articulates with the coalesced neural arches already referred to. The remaining fins are formed quite on the Elasmobranch type, as also is the shoulder-girdle. The right and left halves of the pelvic arch are separate from one another, being united in the middle ventral line by ligament only; each presents a narrow iliac region and a broad, flat pubo-ischial region perforated by two apertures or fenestræ

closed by membrane, one of them of great size in Callorhynchus. The skeleton of the anterior clasper articulates with the pubic region.

Digestive Organs.—The *teeth* (Fig. 802) are very characteristic, having the form of strong plates with an irregular surface and a sharp cutting edge. In the upper jaw there is a pair of small *vomerine teeth* (*vo. t.*) in front, immediately behind them a pair of large *palatine teeth* (*pal. t.*), and in the lower jaw a single

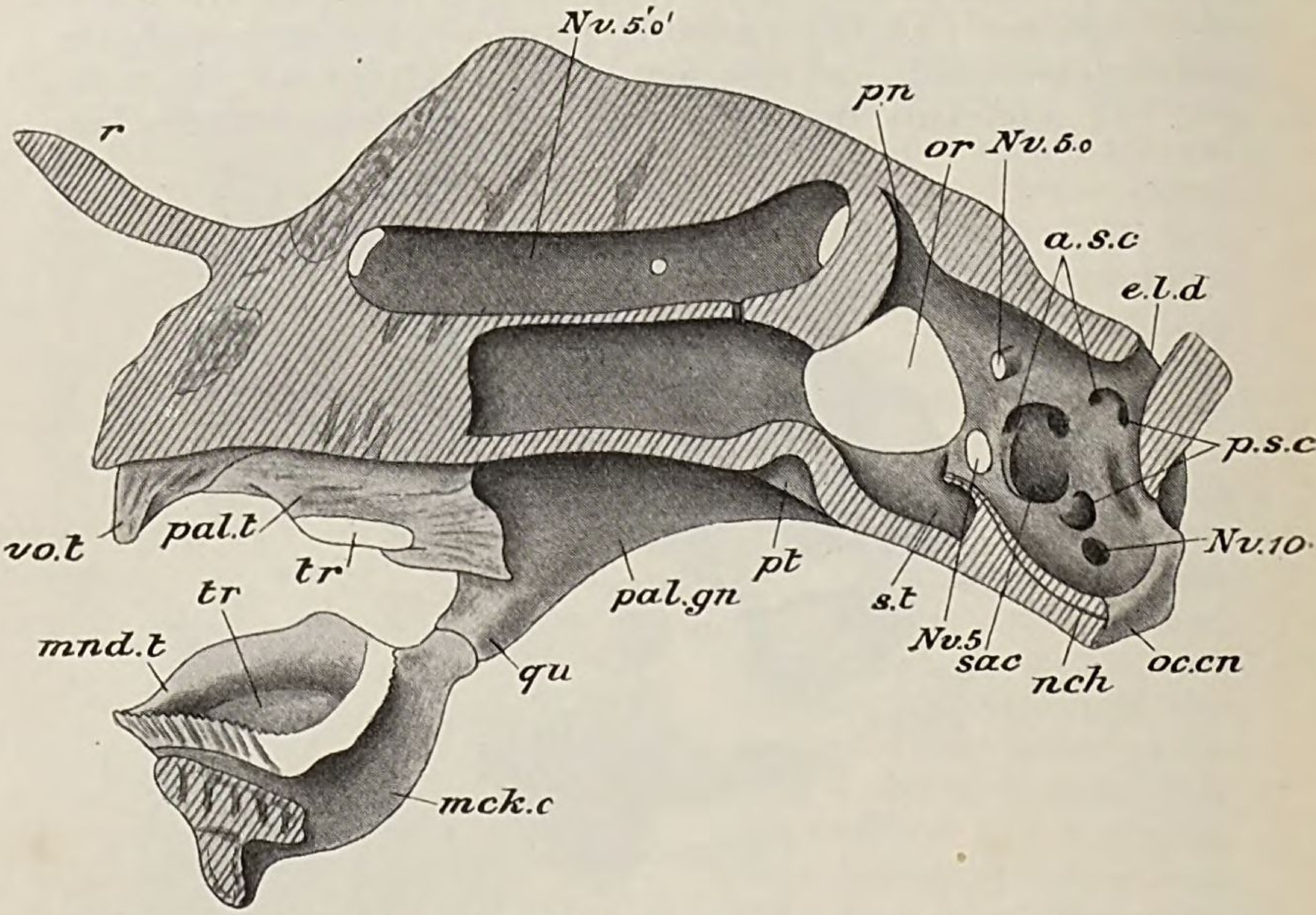


FIG. 802.—**Callorhynchus antarcticus,** sagittal section of skull; the labial cartilages are removed. *a. s. c.* apertures through which the anterior semicircular canal passes from the cranial cavity into the auditory capsule; *e. l. d.* aperture for endolymphatic duct; *mck. c.* Meckel's cartilage; *mnd. t.* mandibular tooth; *nch.* notochord; *Nv. 5*, trigeminal foramen; *Nv. 5. o.* foramen for exit of ophthalmic nerve; *Nv. 5.'o'*, canal for ophthalmic nerves with apertures of entrance and exit; *Nv. 10*, vagus foramen; *oc. cn.* occipital condyle; *or.* fenestra separating cranial cavity from orbit; *pal. qu.* palato-quadrate; *pal. t.* palatine tooth; *pn.* position of pineal body; *pt.* pit for extra-cranial portion of pituitary body; *p. s. c.* apertures through which the posterior semicircular canal passes into the auditory capsule; *qu.* quadrate region of palato-quadrate; *r.* rostrum; *sac.* depression for sacculus; *s. t.* sella turcica; *tr.* tritor; *vo. t.* vomerine teeth.

pair of large *mandibular teeth* (*mnd.t.*). They are composed of vasodentine, and each palatine and mandibular tooth has its surface slightly raised into a rounded elevation of a specially hard substance, of whiter colour than the rest of the tooth, and known as a *tritor* (*tr*). The *stomach* is almost obsolete, the enteric canal passing in a straight line from gullet to anus; there is a well-developed *spiral valve* in the intestine.

Respiratory Organs.—There are three pairs of *holobranchs* or complete gills borne on the first three branchial arches, and two

hemibranchs or half-gills, one on the posterior face of the hyoid, the other on the anterior face of the fourth branchial arch. The fifth branchial arch is, as usual, gill-less, and there is no cleft between it and its predecessor. The gill-filaments are fixed in their whole length to an interbranchial septum, as in Elasmobranchs.

The small **heart** resembles that of the Dog-fish in all essential respects, being formed of sinus venosus, auricle, ventricle, and conus arteriosus, the last with three rows of valves.

The **brain** (Fig. 803), on the other hand, is very unlike that of Scyllium, but presents a fairly close resemblance to that of Scymnus. The medulla oblongata (*med. obl.*) is produced laterally into large frill-like *restiform bodies* (*cp. rst.*), which bound the hinder half of the cerebellum (*cblm*). The diencephalon (*dien.*) is extremely long, trough-shaped, and very thin-walled, having no indication of optic thalami; it is continued without change of diameter into a distinct prosencephalon, which gives off the cerebral hemispheres (*crb. h.*) right and left. The combined di- and prosocœles (*di. cœ.*) are widely open above in a brain from which the membranes have been removed (*A*), but in the entire organ (*B*) are roofed over by a conical, tent-like *choroid plexus* (*ch. plx.* 1). The cavities of the small, spindle-shaped hemispheres (*crb. h.*) communicate with the prosocœle by wide foramina of Monro (*for. M.*), partly blocked up by hemispherical corpora striata (*cp. str.*). Each hemisphere is continued in front into a delicate thin-walled tube, the *olfactory peduncle* (*olf. p.*), bearing at its extremity a compressed olfactory lobe (*olf. l.*).

The optic nerves (*Nv.* 2) form a chiasma. The *pineal body* (*pn. b.*) is a small rounded vesicle borne on a hollow stalk (*pn. s.*) which runs just outside the posterior wall of the tent-like choroid plexus. The *pituitary body* (*pty.*) consists of intra- and extra-cranial portions, the former lodged in the sella turcica, the latter in the pit, already noticed, on the ventral or external face of the skull-floor (Fig. 802, *pt.*). In advanced embryos the two are united by a delicate strand of tissue.

Urino-genital Organs.—The *kidneys* (Fig. 804, *kd.*) are lobed, deep-red bodies, like those of the Dogfish, but shorter and stouter. The female organs, also, are constructed on the Elasmobranch pattern, and are chiefly noticeable for the immense size of the shell-glands and of the uteri. But the male organs present certain quite unique characters. The *testes* (*ts.*) are large ovoid bodies the tubules of which do not contain fully developed sperms, but only immature sperm-cells. These latter are passed through the vasa efferentia into the immense epididymes (*epid.*), where they become aggregated into *spermatophores* in the form of small ovoidal capsules surrounded by a resistent membrane and full of a gelatinous substance in which bundles of sperms are imbedded. The lower

end of the vas deferens (*v. df.*) is dilated to form a large cylindrical *vesicula seminalis* (*vs. sem.*) imperfectly divided into compartments by transverse partitions (*B*) and filled with a greenish jelly. The spermatophores (*sph.*) are passed into these compartments and

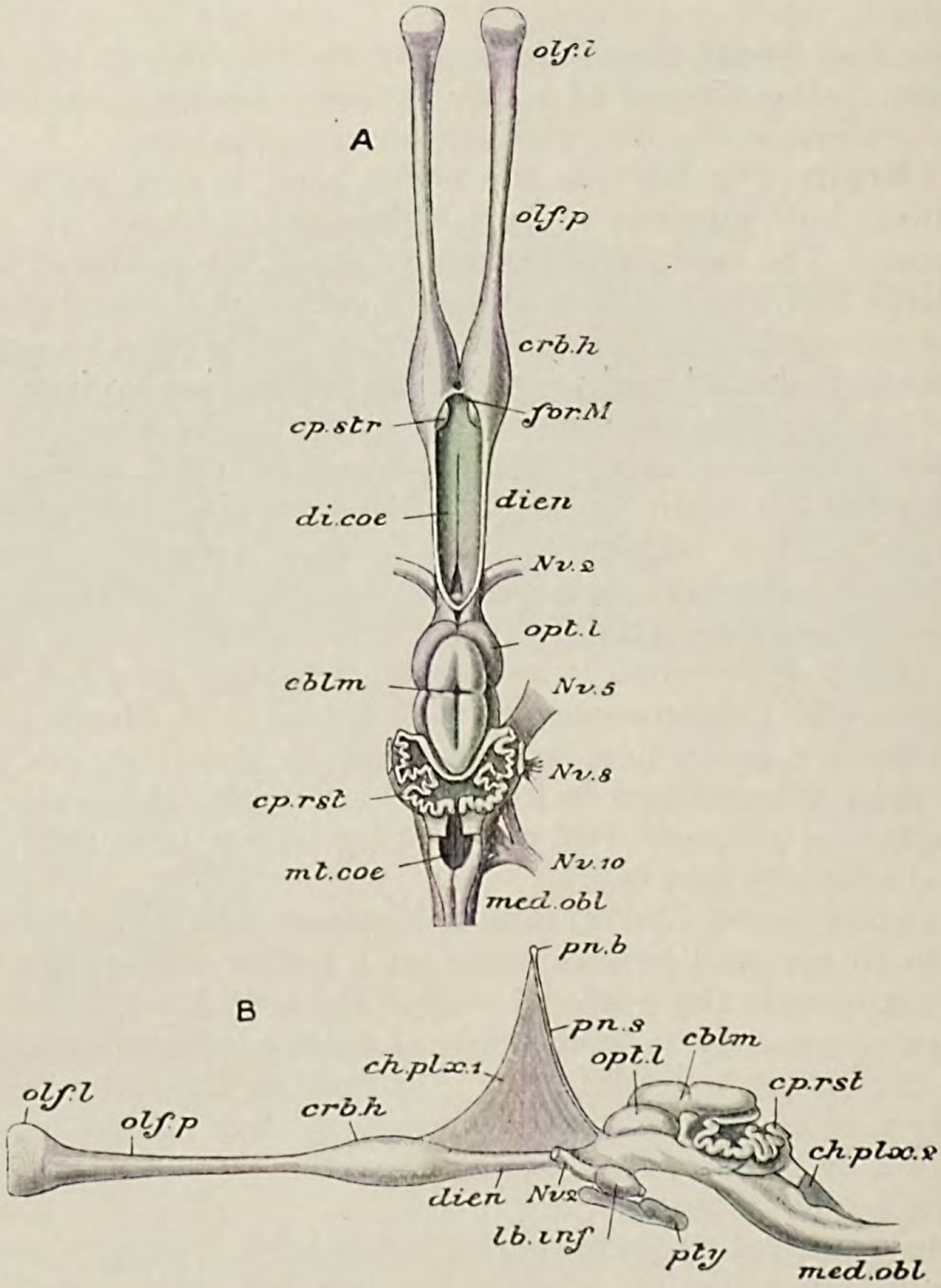


FIG. 803.—**Callorhynchus antarcticus.** A, dorsal view of brain after removal of the membranes; B, side view with the membranes in place. *cblm.* cerebellum; *ch. plx. 1*, choroid plexus of fore-brain; *ch. plx. 2*, of hind-brain; *cp. rst.* corpus restiforme; *cp. str.* corpus striatum; *crb. h.* cerebral hemisphere; *di. coe.* diacœle; *dien.* diencephalon; *for. M.* foramen of Monro; *lb. inf.* lobus inferior; *med. obl.* medulla oblongata; *mt. coe.* metacœle; *Nv. 2*, optic nerve; *Nv. 5*, trigeminal; *Nv. 8*, auditory; *Nv. 10*, vagus; *olf. l.* olfactory lobe; *olf. p.* olfactory peduncle; *opt. l.* optic lobe; *pn. b.* pineal body; *pn. s.* pineal stalk; *pty.* pituitary body.

finally make their way through the central passage into the urino-genital sinus (*u. g. s.*). The vestigial Müllerian ducts (*Mul. d.*) are much more fully developed than in the Dog-fish: they are complete, though narrow, tubes opening behind into the urino-

genital sinus (*Mul. d.″*) and in front by a large common aperture (*Mul. d.′*) into the cœlome.

Development.—Internal impregnation takes place, and the oosperm becomes surrounded, as in the Dog-fish, by a horny egg-shell secreted by the shell-glands. The egg-shell of Callorhynchus

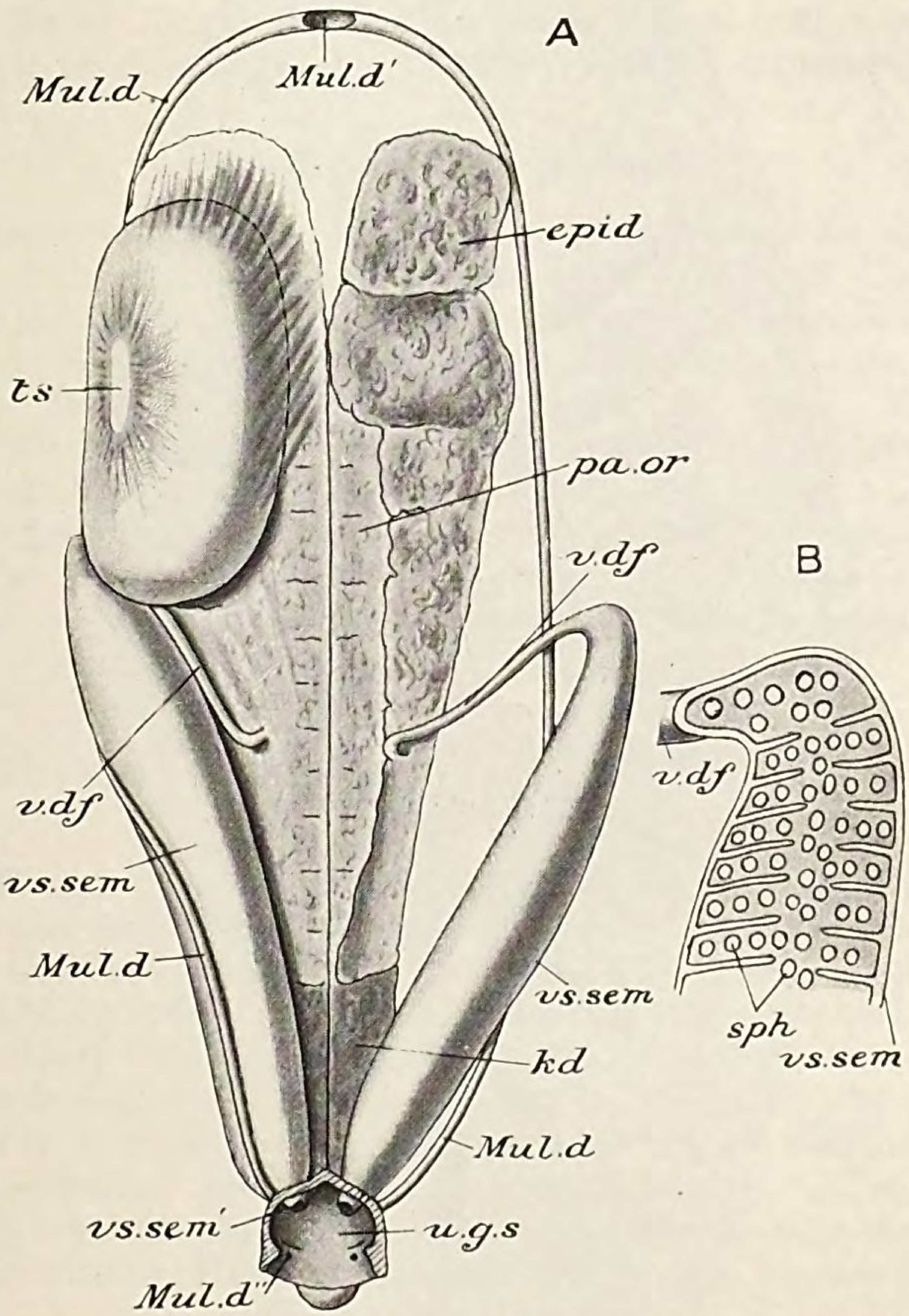


FIG. 804.—**Callorhynchus antarcticus.** A, male urino-genital organs, ventral aspect; the left testis is removed and the left vesicula seminalis displaced; B, anterior part of vesicula seminalis in section. *epid.* epididymis; *kd* kidney; *Mul. d.* Müllerian duct; *Mul. d′.* cœlomic aperture of Müllerian ducts; *Mul. d″.* aperture of Müllerian duct into urino-genital sinus; *pa. or.* anterior (genital) portion of kidney; *sph.* spermatophores; *ts.* testis; *u. g. s.* urino-genital sinus; *v. df.* vas deferens; *vs. sem.* vesicula seminalis; *vs. sem′.* its aperture into urino-genital sinus.

(Fig. 805) is of extraordinary size—about 25 cm. in length, or fully five-sixths as long as the abdominal cavity—and the elongated chamber for the embryo is surrounded by a broad, flat expansion covered on one side with yellow hair-like processes, and giving the shell a close resemblance, doubtless protective, to a

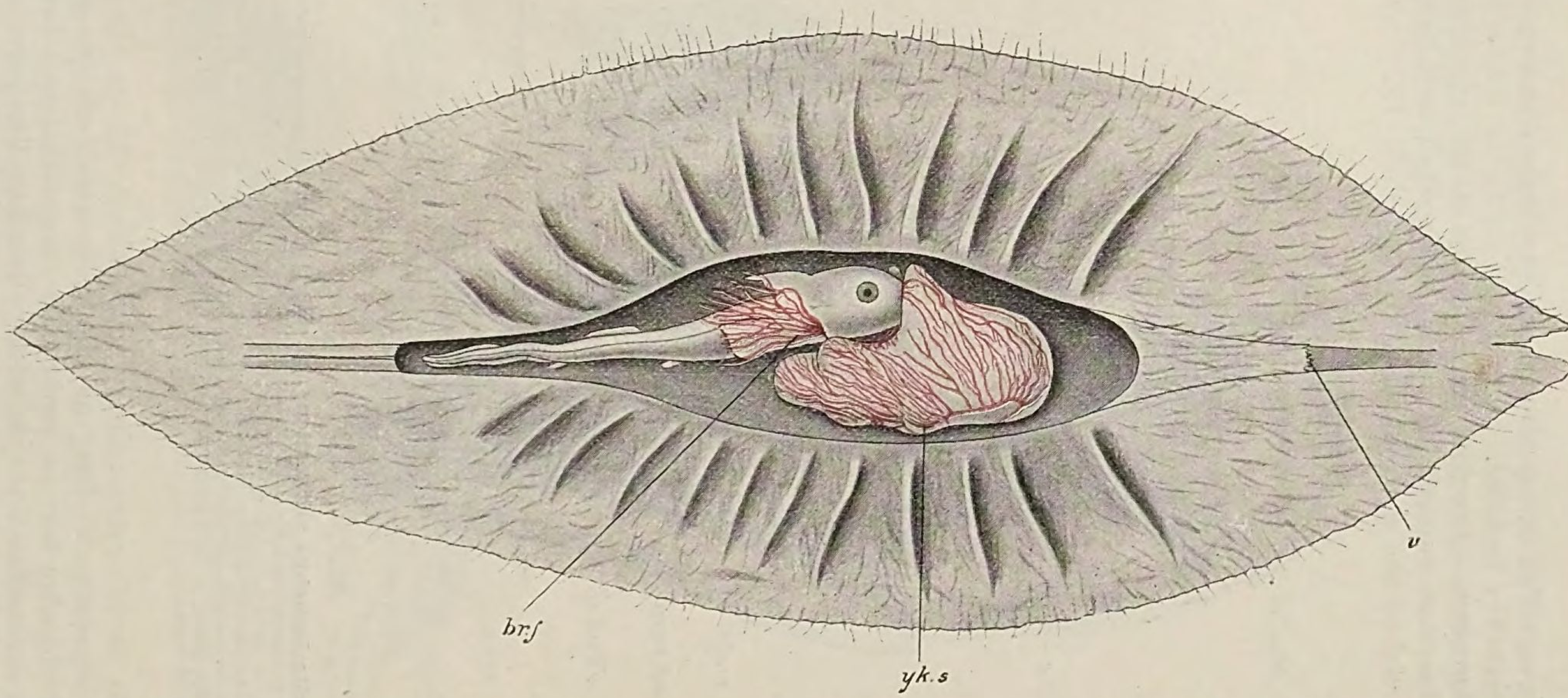


Fig. 805.—**Callorhynchus antarcticus.** Egg-shell with embryonic chamber cut open to show the contained embryo. *br. f.* branchial filaments; *v.* valve through which young fish escapes. *yk. s.* yolk-sac.

piece of kelp. Nothing is known of the early development: the advanced embryo has elongated gill-filaments (*br. f.*) projecting through the branchial aperture, a diphycercal tail, and a curiously lobed and nearly sessile yolk-sac (*yk. s.*).

Fossil remains of Holocephali are known from the lower Jurassic rocks upwards. As might be expected, they consist mostly of teeth and of dorsal fin-spines, but in some cases, and notably in *Squaloraja*, practically the whole of the skeleton is preserved.

Sub-Class III.—Teleostomi.

In this sub-class are included all the commonest and most familiar Fishes, such as the Perch, Pike, Mackerel, Cod, Sole, Herring, Eel, Salmon, etc., as well as the so-called "Ganoid" Fishes, such as the Sturgeon, Bony Pike (*Lepidosteus*) and Bow-fin (*Amia*) of North America, and the *Polypterus* of the Nile. They are distinguished from Elasmobranchs and Holocephali by having the primary skull and shoulder-girdle complicated by the addition of membrane bones, and by possessing bony instead of horn-like fin-rays. The gills are covered by an operculum; the anus is distinct from the urinary and genital apertures; and the brain has no cerebral hemispheres but an undivided prosencephalon.

1. Example of the Sub-class—The Brown Trout (*Salmo fario*).

The Brown Trout is common in the rivers and streams of Europe, and has been acclimatized in other parts of the world, notably in New Zealand. It varies greatly in size, according to the abundance of food and the extent of the water in which it lives: it may attain sexual maturity, and therefore be looked upon as adult, at a length of 18—20 cm. (seven or eight inches), but in large lakes it may grow to nearly a metre in length. Other species of Salmo, such as the Salmon (*S. salar*), the Lake Trout (*S. ferox*), the American Brook Trout (*S. fontinalis*), are common in the Northern Hemisphere and differ only in details from *S. fario*.

External Characters.—The *body* (Fig. 806) is elongated, compressed, thickest in the middle, and tapering both to the head and tail. The *mouth* is terminal and very large: the upper jaw is supported by two freely movable bones, the *premaxilla* (Fig. 807, *pmx.*) in front and the *maxilla* (*mx.*) behind, both bearing sharp curved *teeth* arranged in a single row. When the mouth is opened a row of *palatine teeth* is seen internal and parallel to those of the maxilla, and in the middle line of the roof of the mouth is a double row of *vomerine teeth*. The lower jaw (*md.*) is mainly supported by a bone called the *dentary* and bears a row of teeth: on the throat

each ramus of the mandible is bounded mesially by a deep groove. The floor of the mouth is produced into a prominent *tongue* (*t.*) bearing a double row of teeth. In old males the apex of the lower jaw becomes curved upwards like a hook.

The large *eyes* have no eyelids, but the flat cornea is covered by a transparent layer of skin. A short distance in front of the eye is the double *nostril* (na^1, na^2), each olfactory sac having two apertures, the anterior one (na^1) provided with a flap-like valve. There is no external indication of the ear.

On each side of the posterior region of the head is the *operculum* (Fig. 806, *op.*) or gill-cover, a large flap which, when raised, displays the gills; between it and the flank is the large crescentic gill-opening, from which the respiratory current makes its exit. The operculum is not a mere fold of skin, as in Holocephali, but is supported by four thin bones the outlines of which can be made

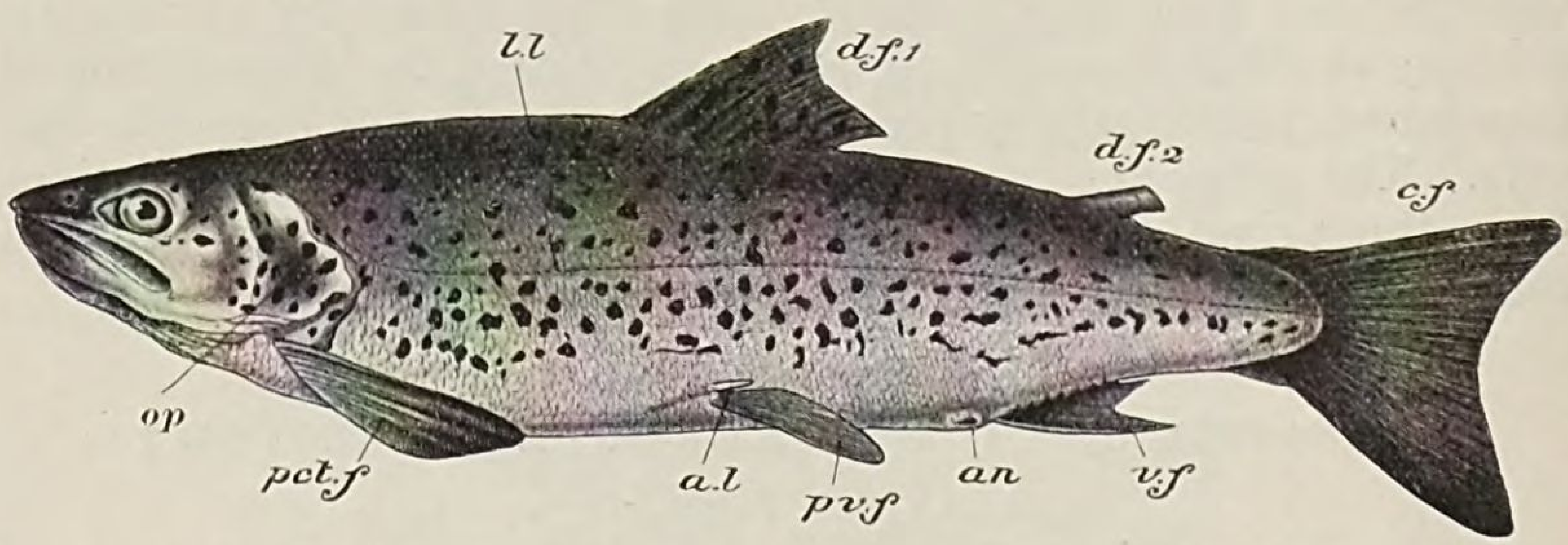


FIG. 806.—**Salmo fario.** *a. l.* adipose lobe of pelvic fin; *an.* anus; *c. f.* caudal fin; *d. f. 1*, first dorsal; *d. f. 2*, second dorsal or adipose fin; *l. l.* lateral line; *op.* operculum; *pct. f.* pectoral fin; *pv. f.* pelvic fin; *v. f.* ventral fin. (After Jardine.)

out through the skin; they are the *opercular* (Fig. 807, *op.*), *pre-opercular* (*p. op.*), *sub-opercular* (*s. op.*), and *inter-opercular* (*i. op.*); the latter is attached to the angle of the mandible. The ventral portion of the operculum is produced into a thin membranous extension, the *branchiostegal membrane* (*br. m.*), supported by twelve flat, overlapping bones, the *branchiostegal rays.* The narrow area on the ventral surface of the throat which separates the two gill-openings from one another is called the *isthmus.* The *gills*, seen by lifting up the operculum, are four red, comb-like organs, each having a double row of free gill filaments; alternating with the gills are the five vertically elongated *gill-slits*, opening into the mouth.

On the ventral surface of the body, at about two-thirds of the distance from the snout to the end of the tail, is the *anus* (Fig. 806, *an.*); behind it is the *urino-genital aperture*, of almost equal size and leading into the *urino-genital sinus*, into which both urinary and genital products are discharged.

The region from the snout to the posterior edge of the operculum is counted as the *head*; the *trunk* extends from the operculum to the anus; the post-anal region is the *tail.*

There are two *dorsal fins:* the *anterior dorsal* (Fig. 806, *d. f.* 1) is large and triangular, and is supported by thirteen bony fin-rays; the *posterior dorsal* (*d. f.* 2) is small and thick, and is devoid of bony supports: it is distinguished as an *adipose fin.* The *caudal fin* (*c. f.*) is the chief organ of locomotion; it differs markedly from that of Elasmobranchs in being, as far as its external appearance is concerned, quite symmetrical, being supported by fin-rays which radiate regularly from the rounded end of the tail proper; such outwardly symmetrical tail-fins are called *homocercal.* There is a single large *ventral fin* (*v. f.*) supported by eleven rays. The *pectoral fin* (*pct. f.*) has fourteen rays and is situated, in the normal position, close behind the gill-opening, but the *pelvic fin* (*pv. f.*) has shifted its position and lies some distance in front of the vent: it is supported by ten rays and has a small process or *adipose lobe* (*a. l.*) springing from its outer edge near the base.

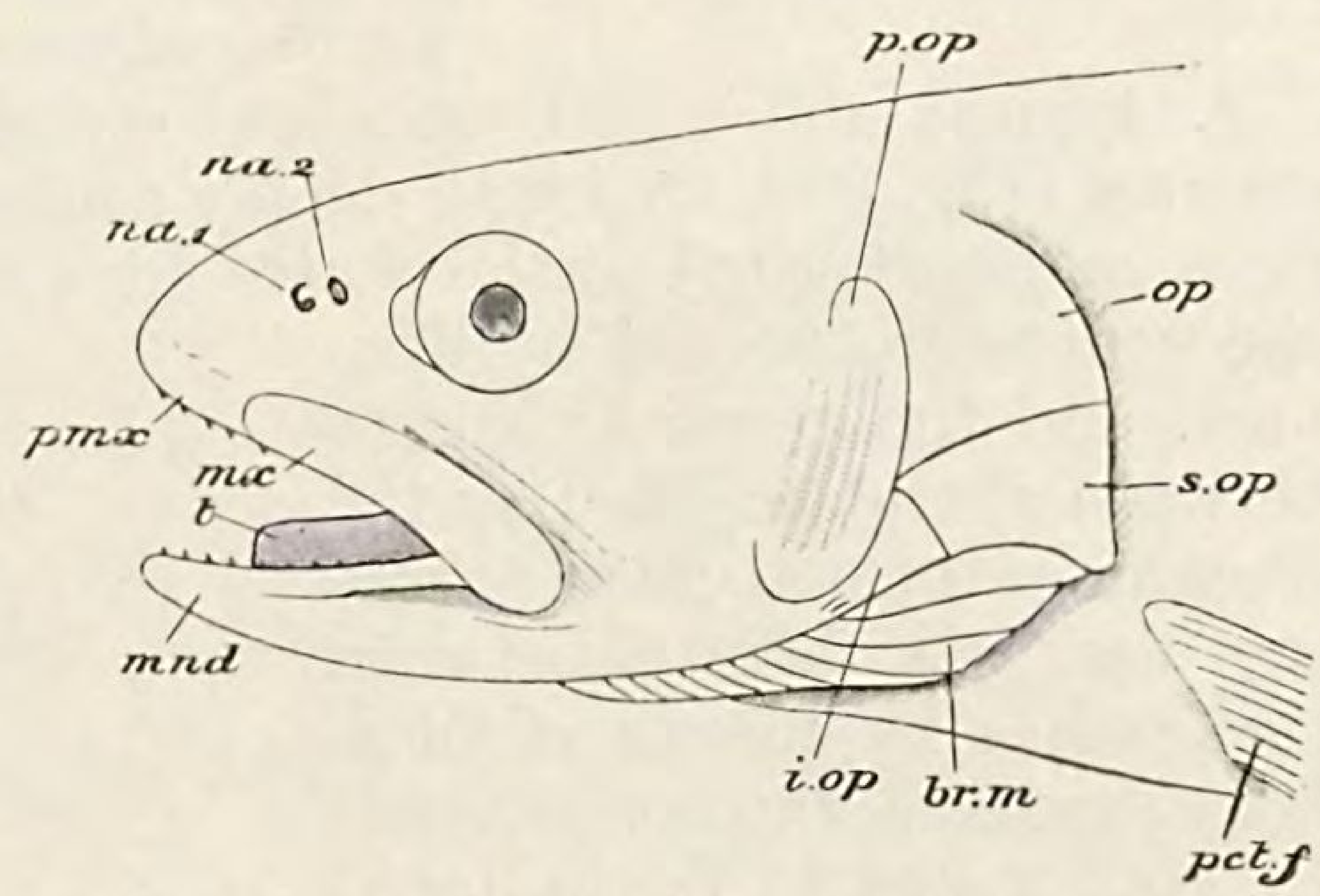


FIG. 807.—Head of female **Salmo fario.** *br. m.* branchiostegal membrane; *i. op.* inter-opercular; *mnd.* mandible; *mx.* maxilla; *na*[1], anterior, and *na*[2], posterior nostril; *op.* opercular; *pct. f.* pectoral fin; *pmx.* premaxilla; *p. op.* pre-opercular; *s. op.* sub-opercular; *t.* tongue.

The body is covered by a soft, slimy *skin* through which, in the trunk and tail, the outlines of the *scales* can be seen; on the head and fins the skin is smooth and devoid of scales. A well-marked *lateral line* (*l. l.*) extends along each side from head to tail. The skin is grey above, shading into yellowish below, and is covered with minute black pigment spots which, on the sides and back, are aggregated to form round spots two or three millimetres in diameter. In young specimens orange-coloured spots are also present.

Skin and Exoskeleton.—The epidermis has no *stratum corneum;* it contains unicellular glands, from which the mucus covering the body is secreted, and pigment cells, to which the colours of the animal are due. The *scales* (Fig. 808) are lodged in pouches of the dermis and have the form of flat, nearly circular plates of bone marked with concentric lines, but having no Haversian canals, lacunæ, or canaliculi. They have an imbricating arrangement, overlapping one another from before backwards,

like the tiles of a house, in such a way that a small three-sided portion (*b*) of each scale comes to lie immediately beneath the epidermis, while the rest (*a*) is hidden beneath the scales immediately anterior to it. Besides the scales, the fin-rays belong to the exoskeleton, but will be most conveniently considered in connection with the endoskeleton.

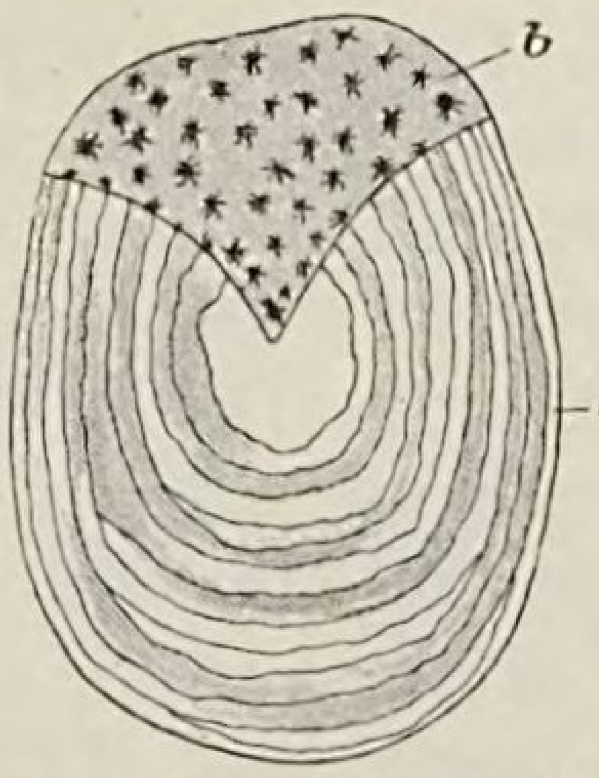


FIG. 808.—Scale of **Salmo fario.** *a.* anterior portion covered by overlap of preceding scales; *b*, free portion covered only by pigmented epidermis.

Endoskeleton.—The *vertebral column* shows a great advance on that of the two previous classes in being thoroughly differentiated into distinct bony *vertebræ.* It is divisible into an anterior or *abdominal region* and a posterior or *caudal region*, each containing about twenty-eight vertebræ.

A typical abdominal vertebra consists of a dice-box-shaped *centrum* (Fig. 809, CN.) with deeply concave anterior and posterior faces, and perforated in the centre by a small hole. The edges of the centra are united by ligament and the biconvex spaces between them are filled by the remains of the notochord; there are also articulations between the arches by means of little bony processes, the *zygapophyses* (N. ZYG., H. ZYG.). To the dorsal surface of the centrum is attached, by ligaments in the anterior vertebræ, by *ankylosis* or actual bony union in the posterior, a low *neural arch* (N. A.), which consists in the anterior vertebræ of distinct right and left moieties and is continued above into a long, slender, double *neural spine* (N. SP.), directed upwards and backwards. To the ventro-lateral region of the vertebra are attached by ligament a pair of long, slender *ribs* (R.) with dilated heads, which curve downwards and backwards between the muscles and the peritoneum, thus encircling the abdominal cavity. In the first two vertebræ they are attached directly to the centrum, in the

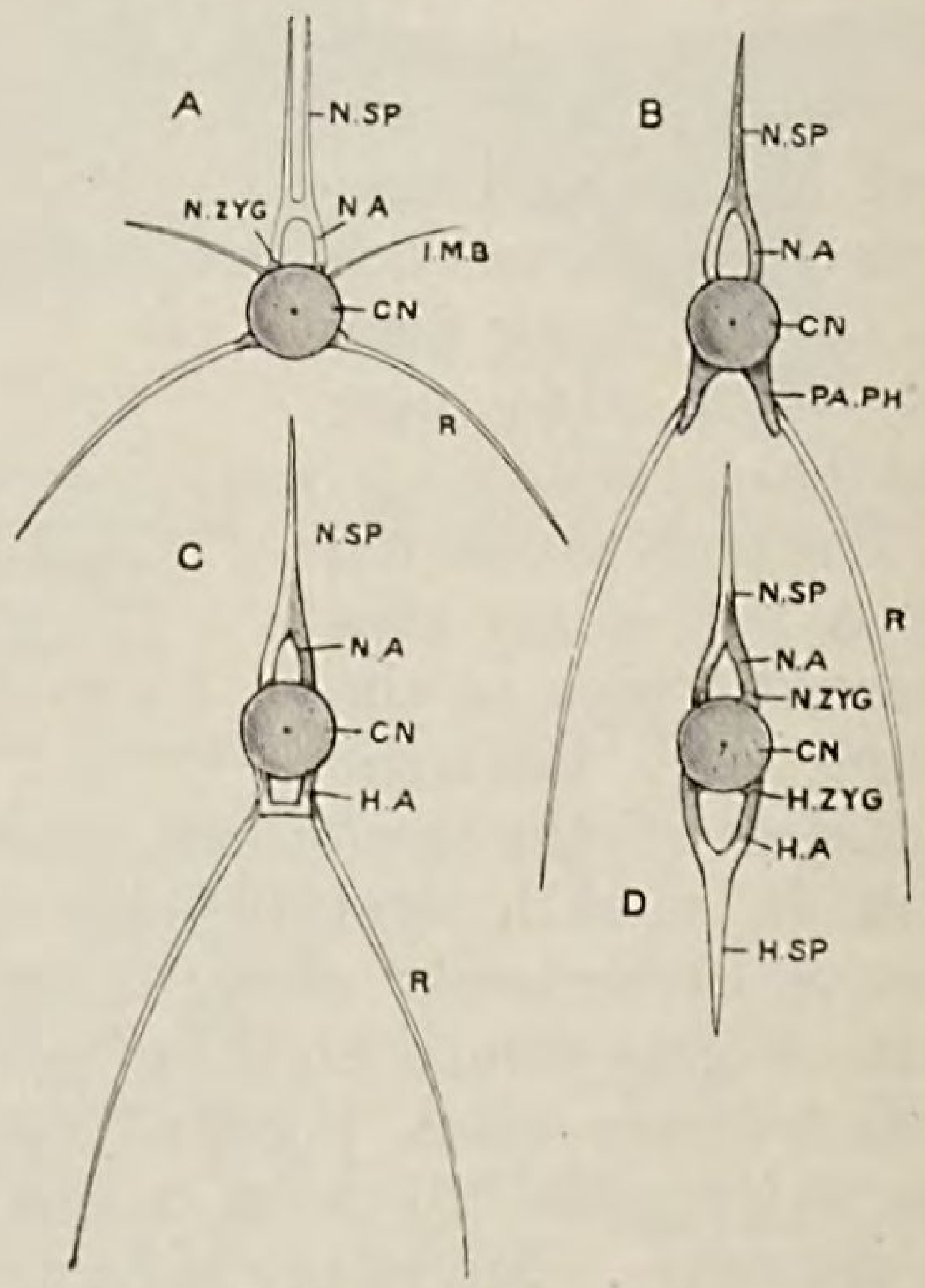


FIG. 809.—**Salmo fario.** A, one of the anterior, and B, one of the posterior abdominal vertebræ; C, one of the anterior, and D, one of the posterior caudal vertebræ. **CN.** centrum; **IMB.** inter-muscular bone; **HA.** hæmal arch; **H. SP.** hæmal spine; **H. ZYG.** hæmal zygapophysis; **N. A.** neural arch; **N. SP.** neural spine; **N. ZYG.** neural zygapophysis; **PA. PH.** parapophysis; **R.** rib.

rest to short downwardly directed bones, the *parapophyses* (PA. PH.) immovably articulated by broad surfaces to the centrum. At the junction of the neural arch with the centrum are attached, also by fibrous union, a pair of delicate *inter-muscular bones* (I. M. B.) which extend outwards and backwards in the fibrous septa between the myomeres. The first and second abdominal vertebræ bear no ribs. In the last three the neural spines (N. SP.) are single.

In the caudal vertebræ the outgrowths corresponding to the parapophyses are fused with the centrum and unite in the middle ventral line, forming a *hæmal arch* (C, H. A.), through which the caudal artery and vein run. In the first six caudals each hæmal arch bears a pair of ribs (R.), in the rest the arch is produced downwards and backwards into a *hæmal spine* (D, H. SP.).

The centra as well as the arches of the vertebræ are formed entirely from the skeletogenous layer, and not from the sheath of the notochord as in Elasmobranchs (see pp. 66 and 137).

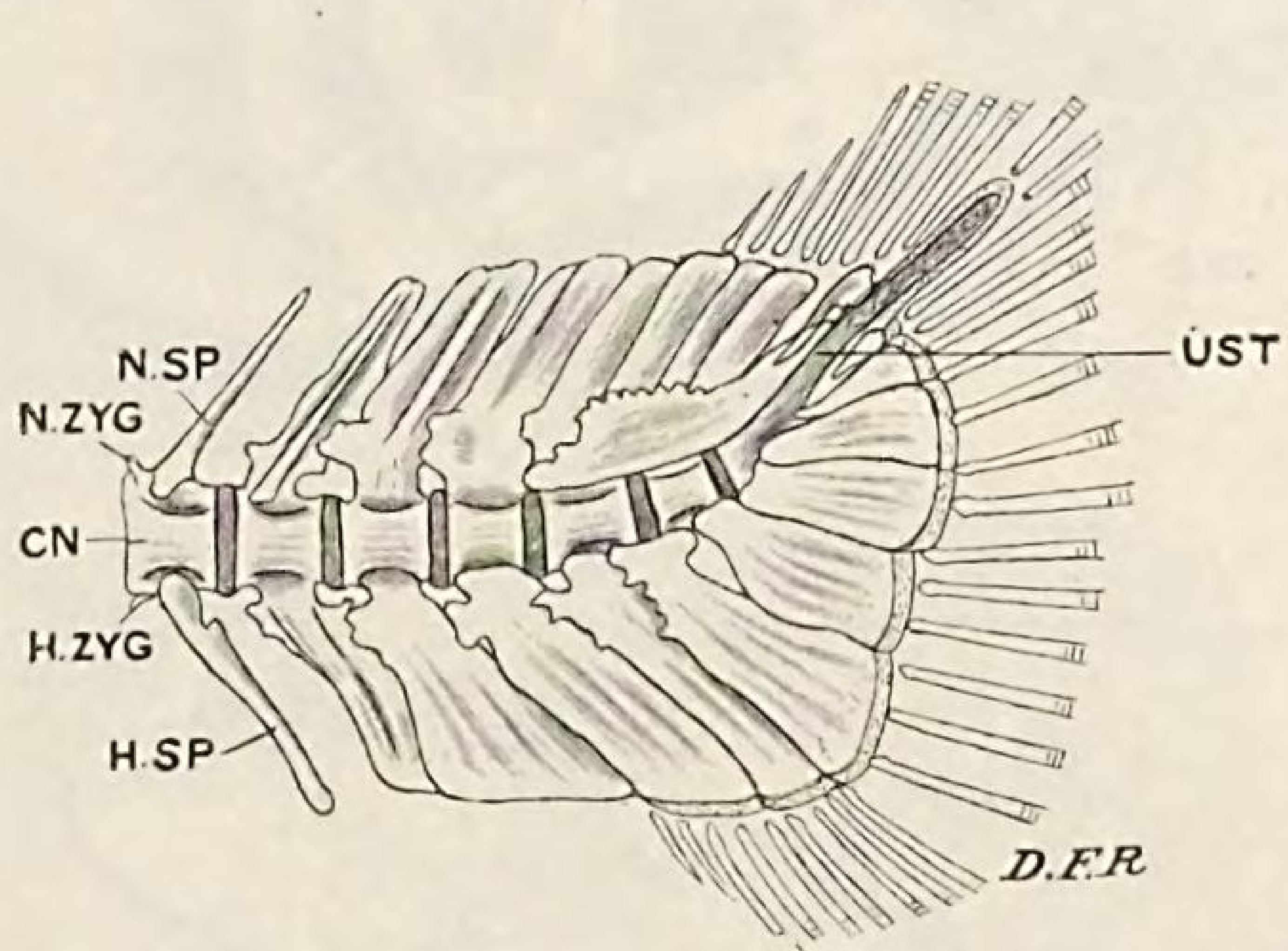


FIG. 810.—**Salmo fario,** caudal end of vertebral column. **CN.** centrum; *D. F. R.* dermal fin-rays; **H. SP.** hæmal spine; **H. ZYG.** hæmal zygapophysis; **N. SP.** neural spine; **N. ZYG.** neural zygapophysis; **UST.** urostyle.

The posterior end of the caudal region is curiously modified for the support of the tail-fin. The hindmost centra (Fig. 810, CN.) have their axes not horizontal but deflected upwards, and following the last undoubted centrum is a rod-like structure, the *urostyle* (UST), consisting of the partly ossified end of the notochord, which has thus precisely the same upward flexure as in the Dog-fish. The neural and hæmal spines (N.SP., H.SP.) of the last five vertebræ are very broad and closely connected with one another, and are more numerous than the centra; and three or four hæmal arches are attached to the urostyle. In this way a firm vertical plate of bone is formed, to the edge of which the caudal fin-rays (*D.F.R.*) are attached fan-wise in a symmetrical manner. It will be obvious, however, that this homocercal tail-fin is really quite as unsymmetrical as the heterocercal fin of the Dog-fish, since, its morphological axis being constituted by the notochord, nearly the whole of its rays are, in strictness, ventral.

The *skull* (Fig. 811) is an extremely complex structure, composed of mingled bone and cartilage. The cartilage has no superficial mosaic of lime-salts such as we find in Elasmobranchs, but

certain portions of it are replaced by cartilage bones, and there are in addition numerous membrane-bones developed in the surrounding connective tissue. As in the Dog-fish, the skull may be divided into cranium, upper and lower jaws, with their suspensory apparatus, and hyoid and branchial arches.

The *cranium* (Fig. 812) is a somewhat wedge-shaped structure its apex being directed forwards. At first sight the distinction between cartilage and membrane-bones is not obvious, but after

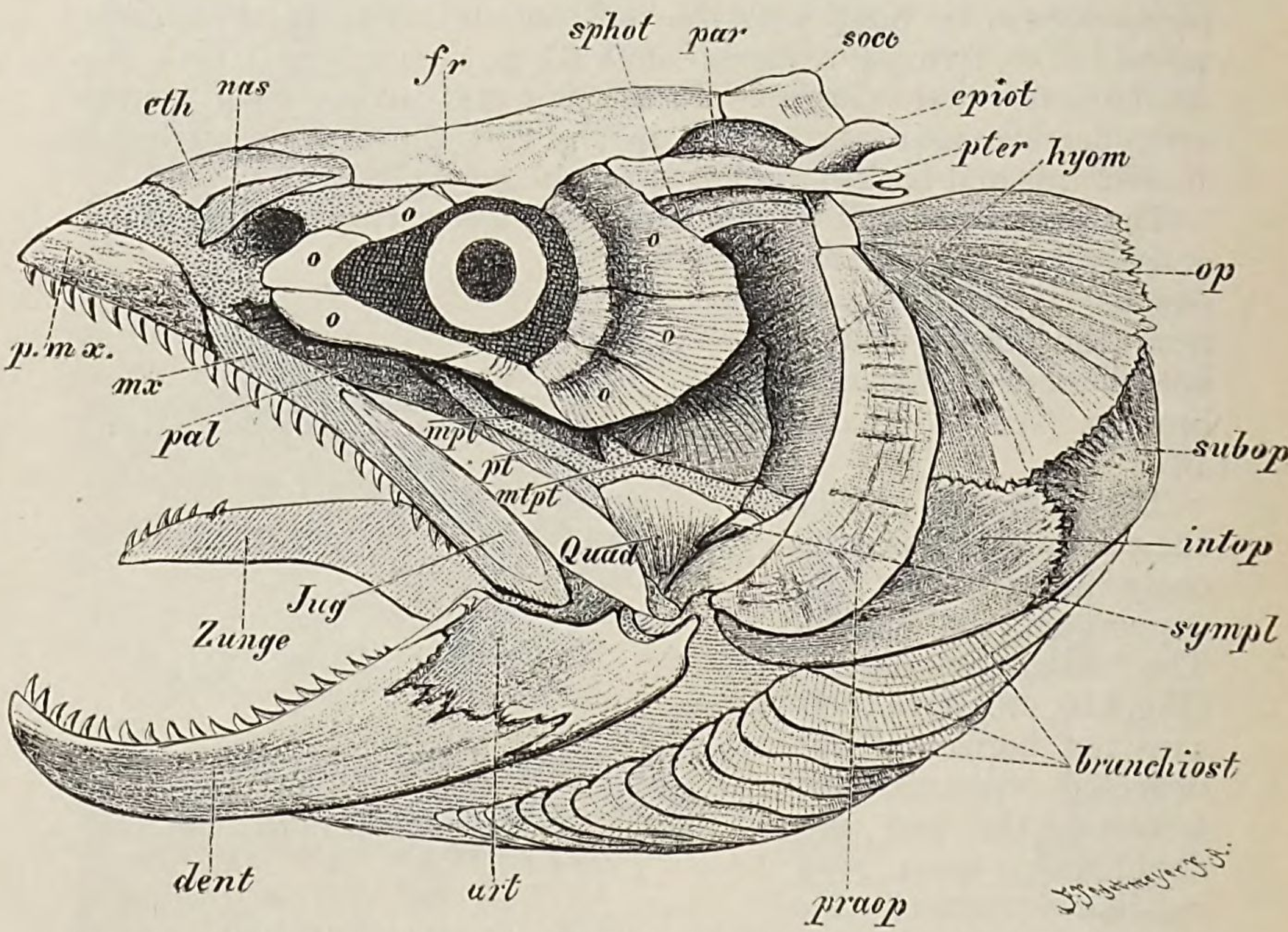


FIG. 811.—**Salmo fario,** the entire skull, from the left side. *art.* articular; *branchiost.* branchiostegal rays; *dent.* dentary; *epiot.* epiotic; *eth.* supra-ethnoid; *fr.* frontal; *hyom.* hyomandibular; *intop.* inter-opercular; *Jug.* jugal; *mpt.* mesopterygoid; *mtpt.* metapterygoid; *mx.* maxilla; *nas.* nasal; *o.* sub-orbitals; *op.* opercular; *pal.* palatine; *par.* parietal; *pmx.* pre-maxilla; *praop.* pre-opercular; *pt.* pterygoid; *pter.* pterotic; *Quad.* quadrate; *socc.* supra-occipital; *sphot.* sphenotic; *subop.* sub-opercular; *sympl.* symplectic; *Zunge*, basihyal. (From Wiedersheim's *Vertebrata.*)

maceration or boiling certain flat bones (the paired parietals, *PA.*, frontals, *FR.*, and nasals, *NA.*, and the unpaired supra-ethmoid, *S.ETH.*) can be easily removed from the dorsal surface; and two unpaired bones (the parasphenoid, *PA. SPH.*, and vomer, *VO.*) from the ventral surface. These are all membrane-bones: they are simply attached to the cranium by fibrous tissue, and can readily be prised off when the latter is sufficiently softened by maceration or boiling. We thus get a distinction between the cranium as a whole, or *secondary cranium*, complicated by the presence of mem-

brane-bones, and the *primary cranium* or *chondrocranium*, left by the removal of these bones and corresponding exactly with the cranium of a Dog-fish.

The primary cranium contains the same regions as that of Scyllium. Posteriorly is the *occipital region*, surrounding the foramen magnum, presenting below that aperture a single concave *occipital condyle* for the first vertebra, and produced above into an

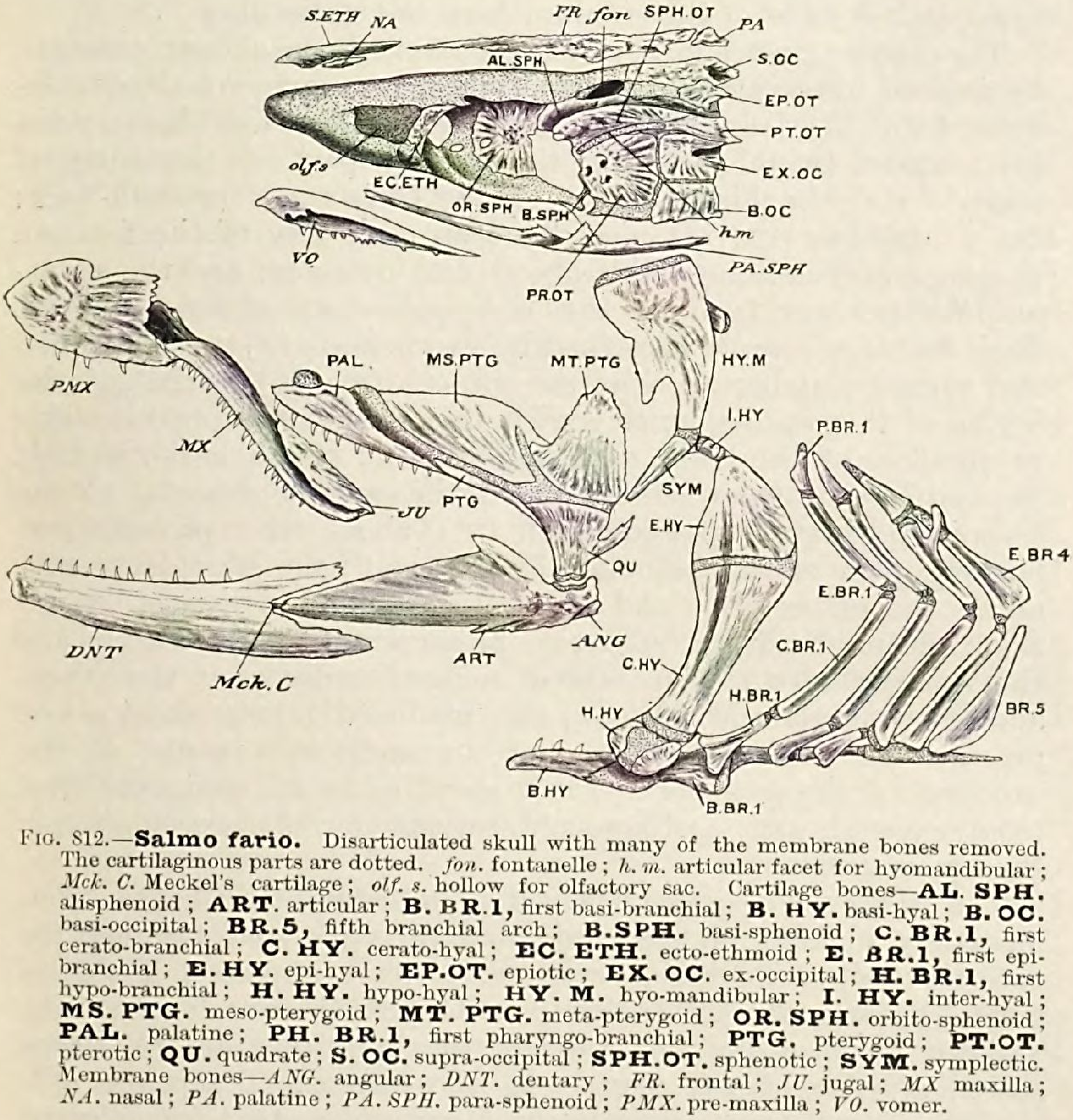


FIG. 812.—**Salmo fario.** Disarticulated skull with many of the membrane bones removed. The cartilaginous parts are dotted. *fon.* fontanelle; *h. m.* articular facet for hyomandibular; *Mck. C.* Meckel's cartilage; *olf. s.* hollow for olfactory sac. Cartilage bones—**AL. SPH.** alisphenoid; **ART.** articular; **B. BR.1,** first basi-branchial; **B. HY.** basi-hyal; **B. OC.** basi-occipital; **BR.5,** fifth branchial arch; **B.SPH.** basi-sphenoid; **C. BR.1,** first cerato-branchial; **C. HY.** cerato-hyal; **EC. ETH.** ecto-ethmoid; **E. BR.1,** first epi-branchial; **E. HY.** epi-hyal; **EP.OT.** epiotic; **EX. OC.** ex-occipital; **H. BR.1,** first hypo-branchial; **H. HY.** hypo-hyal; **HY. M.** hyo-mandibular; **I. HY.** inter-hyal; **MS. PTG.** meso-pterygoid; **MT. PTG.** meta-pterygoid; **OR. SPH.** orbito-sphenoid; **PAL.** palatine; **PH. BR.1,** first pharyngo-branchial; **PTG.** pterygoid; **PT.OT.** pterotic; **QU.** quadrate; **S. OC.** supra-occipital; **SPH.OT.** sphenotic; **SYM.** symplectic. Membrane bones—*ANG.* angular; *DNT.* dentary; *FR.* frontal; *JU.* jugal; *MX* maxilla; *NA.* nasal; *PA.* palatine; *PA. SPH.* para-sphenoid; *PMX.* pre-maxilla; *VO.* vomer.

occipital crest. The *auditory capsules* project outwards from the occipital region, and between them on the dorsal surface of the skull are paired oval *fontanelles* (*fon.*) closed in the entire skull by the frontal bones. The posterior region of the cranial floor is produced downwards into paired longitudinal ridges, enclosing between them a groove which is converted into a canal by the apposition of the parasphenoid bone and serves for the origin of the

eye-muscles. In front of the auditory region the cranium is excavated on each side by a large *orbit*, a vertical plate or *interorbital septum* (OR. SPH.) separating the two cavities from one another. In front of the orbital region the cranium broadens out to form the *olfactory capsules*, each excavated by a deep pit (*olf. s.*) for the olfactory sac, and anterior to these is a blunt snout or *rostrum*. The occipital region is formed as usual from the parachordals of the embryonic skull, the auditory region from the auditory capsules, and the rest of the cranium from the trabeculæ.

The cartilage bones, formed as ossifications in the chondrocranium, correspond in essentials with the typical arrangement already described (p. 72). In the occipital region are four bones; the *basi-occipital* (B. OC.), forming the greater part of the occipital condyle and the hinder region of the *basis cranii* or skull-floor: the *ex-occipitals* (EX. OC.), placed one on each side of the foramen magnum and meeting both above and below it; and the *supra-occipital* (S. OC.) forming the occipital crest already noticed. Each auditory capsule is ossified by five bones—*i.e.*, two more than the typical number (p. 72); the *pro-otic* (PR. OT.) in the anterior region of the capsule, uniting with its fellow of the opposite side in the floor of the brain case, just in front of the basi-occipital; the *opisthotic*, in the posterior part of the capsule, external to the ex-occipital; the *sphenotic* (SPH. OT.), above the pro-otic and forming part of the boundary of the orbit; the *pterotic* (PT. OT.), above the ex-occipital and opisthotic, forming a distinct lateral ridge and produced behind into a prominent *pterotic process;* and the *epiotic* (EP. OT.), a small bone, wedged in between the supra- and ex-occipitals and pterotic, and produced into a short *epiotic process.* On the external face of the auditory capsule, at the junction of the pro-, sphen-, and pterotics, is an elongated facet (*h.m.*) covered with cartilage and serving for the articulation of the hyo-mandibular.

The trabecular region of the cranium contains six bones. Immediately in front of the conjointed pro-otics, and forming the anterior end of the basis cranii, is a small unpaired Y-shaped bone, the *basi-sphenoid* (B. SPH.). Above it, and forming the anterior parts of the side-walls of the brain-case, are the large paired *alisphenoids* (AL. SPH.). In the interorbital septum is a median vertical bone, representing fused *orbitosphenoids* (OR. SPH.). Lastly, in the posterior region of each olfactory capsule, and forming part of the boundary of the orbit, is the *ecto-ethmoid* (EC. ETH.).

The membrane bones already referred to are closely applied to the roof and floor of the chondrocranium, and modify its form considerably by projecting beyond the cartilaginous part, and concealing apertures and cavities. The great *frontals* (*FR.*) cover the greater part of the roof of the skull, concealing the fontanelles, and

furnishing roofs to the orbits. Immediately behind the frontals is a pair of very small *parietals* (*PA.*), in front of them is an unpaired *supra-ethmoid* (*S. ETH.*), to the sides of which are attached a pair of small *nasals* (*NA.*). On the ventral surface is the large *para-sphenoid* (*PA. SPH.*), which forms a kind of clamp to the whole cartilaginous skull floor; and in front of and below the parasphenoid is the toothed *vomer* (*VO.*). Encircling the orbit is a ring of scale-like bones, the *sub-orbitals*. (Fig. 811, *o.*).

In the jaws, as in the cranium, we may distinguish between primary and secondary structures. The primary upper jaw or *palato-quadrate* is homologous with the upper jaw of the Dog-fish, but instead of remaining cartilaginous, it is ossified by five cartilage bones: the toothed *palatine* (PAL.) in front, articulating with the olfactory capsule: then the *pterygoid* (PTG.) on the ventral and the *meso-pterygoid* (MS. PTG.) on the dorsal edge of the original cartilaginous bar: the *quadrate* (QU.) at the posterior end of the latter, furnishing a convex condyle for the articulation of the lower jaw: and projecting upwards from the quadrate the *meta-pterygoid* (MT. PTG.). These bones do not, however, enter into the gape, and do not therefore constitute the actual upper jaw of the adult fish: external to them are two large membrane bones, the *premaxilla* (*PMX.*) and the *maxilla* (*MX.*), which together form the actual or secondary upper jaw; they both bear teeth. A small scale-like bone, the *jugal* (*JU.*) is attached to the posterior end of the maxilla.

The lower jaw is similarly modified. Articulating with the quadrate is a large bone, the *articular* (ART.) continued forwards by a narrow pointed rod of cartilage: the latter is the unossified distal end of the primary lower jaw or Meckel's cartilage, the articular is its ossified proximal end, and therefore a cartilage bone. Ensheathing Meckel's cartilage and forming the main part of the secondary lower jaw is a large toothed membrane bone, the *dentary* (*DNT.*), and a small membrane bone, the *angular* (*ANG.*) is attached to the lower and hinder end of the articular.

The connection of the upper jaw with the cranium is effected partly by the articulation of the palatine with the olfactory region, partly by means of a *suspensorium* formed of two bones separated by a cartilaginous interval: the larger, usually called the *hyo-mandibular* (HY. M.), articulates with the auditory capsule by the facet already noticed, and the small pointed *symplectic* (SYM.), fits into a groove in the quadrate. Both bones are attached by fibrous tissue to the quadrate and metapterygoid, and in this way the suspensorium and palato-quadrate together form an inverted arch, freely articulated in front with the olfactory, and behind with the auditory capsule and thus giving rise to an extremely mobile upper jaw. As its name implies, the hyo-mandibular (together with the symplectic) is commonly held to be the upper

end of the hyoid arch and the homologue of the hyo-mandibular of Elasmobranchs, but there is some reason for thinking that it really belongs to the mandibular arch, and corresponds with the dorsal and posterior part of the triangular palato-quadrate of Holocephali: a perforation in the latter would convert it into an inverted arch having the same general relations as the upper jaw *plus* suspensorium of the Trout, but fused, instead of articulated, with the cranium at either extremity.

The hyoid cornu is articulated to the cartilaginous interval between the hyo-mandibular and symplectic through the intermediation of a small, rod-like bone, the *inter-hyal* (I. HY.), which perhaps represents the hyo-mandibular of Elasmobranchs. It is ossified by three bones: an *epi-hyal* (E. HY.) above, then a large *cerato-hyal* (C. HY.), and below a small double *hypo-hyal* (H. HY.). The right and left hyoid bars are connected by a keystone-piece, the unpaired, toothed *basi-hyal* (B. HY.), which supports the tongue.

Connected with the hyo-mandibular and hyoid cornu are certain membrane-bones serving for the support of the operculum. The *opercular* (Fig. 811, *op.*) is articulated with a backward process of the hyo-mandibular, the *pre-opercular* (*pra-op.*) lies outside the posterior border of the hyo-mandibular and quadrate, and clamps them together; the *sub-opercular* (*sub-op.*) is below and internal to the opercular; and the *inter-opercular* (*int.-op.*) fits between the lower portions of the three preceding bones, and is attached by ligament to the angle of the mandible. The ten sabre-shaped *branchiostegal rays* (*branchiost.*) are attached along the posterior border of the epi- and cerato-hyal, and below the basi-hyal is an unpaired bone, the *basi-branchiostegal* or *uro-hyal*.

There are five branchial arches, diminishing in size from before backwards. The first three present the same segments as in the Dog-fish: *pharyngo-branchial* (PH. BR.) above, then *epi-branchial* (E. BR.), then a large *cerato-branchial* (C. BR.), and a small *hypo-branchial* (H. BR.) below. The right and left hypobranchials of each arch are connected by an unpaired *basi-branchial* (B. BR.). All these segments are ossified by cartilage bones, and the basi-branchials are connected with one another and with the basi-hyal by cartilage, so as to form a median ventral bar in the floor of the pharynx. In the fourth arch the pharyngo-branchial is unossified, and the hypo-branchial absent, and the fifth arch (BR.5) is reduced to a single bone on each side. Small spine-like ossifications are attached in a single or double row along the inner aspect of each of the first four arches: these are the *gill-rakers;* they serve as a sieve to prevent the escape of food by the gill-slits.

The comparison of this singularly complex skull with the comparatively simple one of the Dog-fish is much facilitated by the examination of the skull of a young Trout or Salmon. In the

latter, at about the second week after hatching, the only ossifications present are a few membrane bones; when these are removed we get a purely cartilaginous skull (Fig. 813), exactly comparable with that of an Elasmobranch. There is a cranium devoid of cartilage bones and divisible only into regions; the upper jaw is an unossified palato-quadrate (*Pl. Pt.*, *M. Pt.*, *Qu.*) and the lower jaw (*Mck.*) a large Meckel's cartilage; the suspensorium is an undivided hyo-mandibular (*HM.*), and the hyoid and branchial arches are unsegmented.

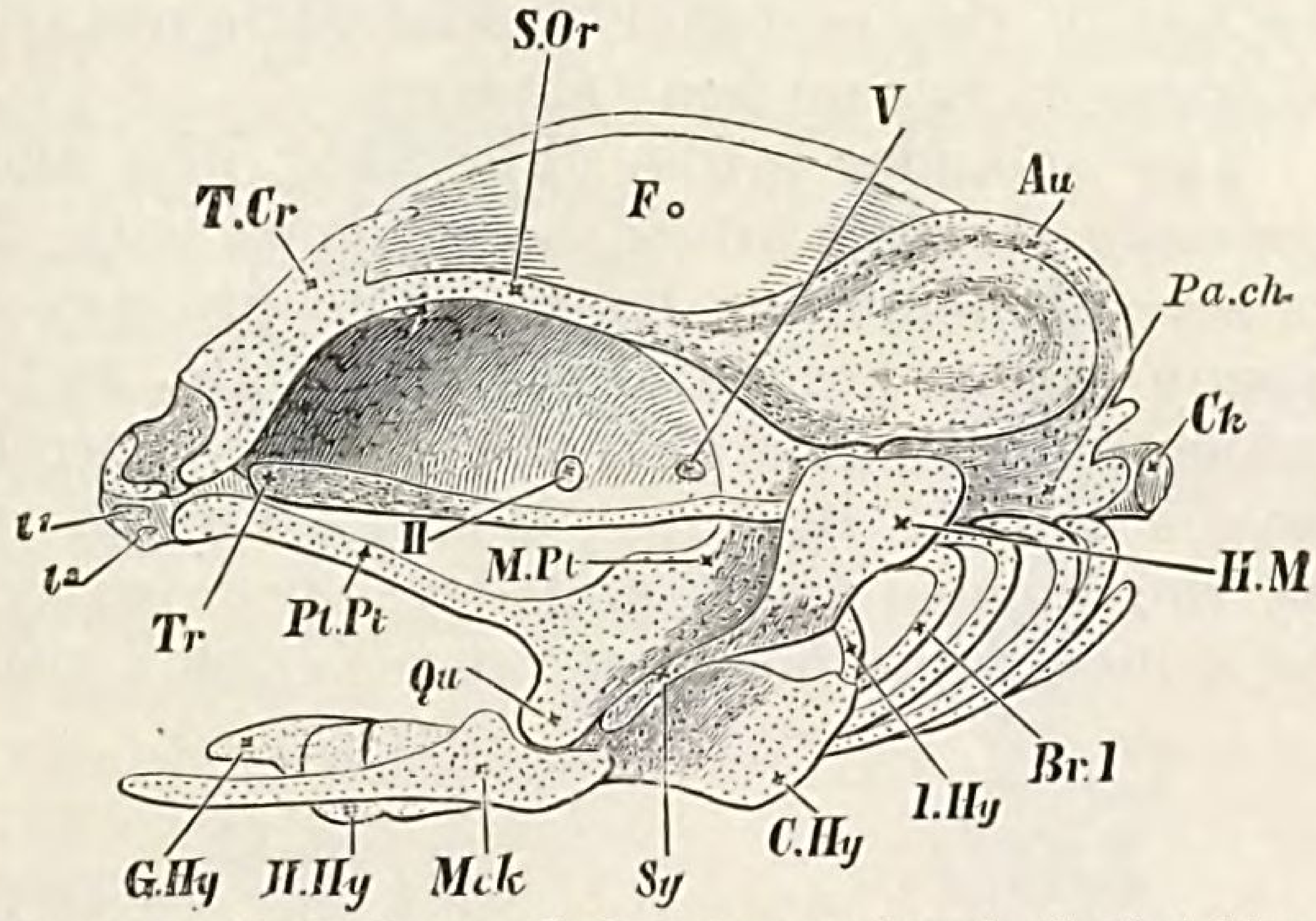


FIG. 813.—Skull of young **Salmon**, second week after hatching; the membrane bones removed. *Au.* auditory capsule; *Br. 1*, first branchial arch; *Ch.* notochord; *C. Hy.* hyoid cornu; *Fo.* fontanelle; *G. Hy.* basi-hyal; *H. Hy.* hypo-hyal; *H. M.* hyomandibular; *I. Hy.* inter-hyal; l^1, l^2, labial cartilages; *Mck.* Meckel's cartilage; *M. Pt.* meta-pterygoid region of primary upper jaw; *Pa. ch.* parachordal; *Pl. Pt.* palato-pterygoid region; *Qu.* quadrate region; *S.Or.* supra-orbital region of cranium; *Sy.* symplectic region of suspensorium; *T. Cr.* cranial roof; *Tr.* trabecula; *II*, optic foramen; *V*, trigeminal foramen. (From Parker and Bettany's *Morphology of the Skull.*)

The *first dorsal* and the *ventral fins* are supported each by a triple set of pterygiophores, so that the fin-skeleton is multiserial, as in the Dog-fish. The proximal series consists of slender bony rays—the *interspinous bones* (Fig. 817, PTG.; Fig. 814, PTG.1), lying in the median plane, between the muscles of the right and left sides, and more numerous than the myomeres of the regions in which they occur. Their distal ends are broadened, and with them are connected the second series (PTG.2) in the form of small dice-box shaped bones; to these, finally, are attached small nodules of cartilage (*ptg.3*) forming the third series of radials. The *dermal fin-rays* (*D.F.R.*), which lie in the substance of the fin itself, are slender bones, jointed like the antennæ of an Arthropod, and mostly branched in the sagittal plane (Fig. 817, *D.F.R.*). Each is formed of distinct right and left pieces (Fig. 814), in close contact for the most part, but diverging below to form a forked and dilated end, which fits over one of the cartilaginous nodules (*ptg.3*). In the caudal fin (Fig. 810)

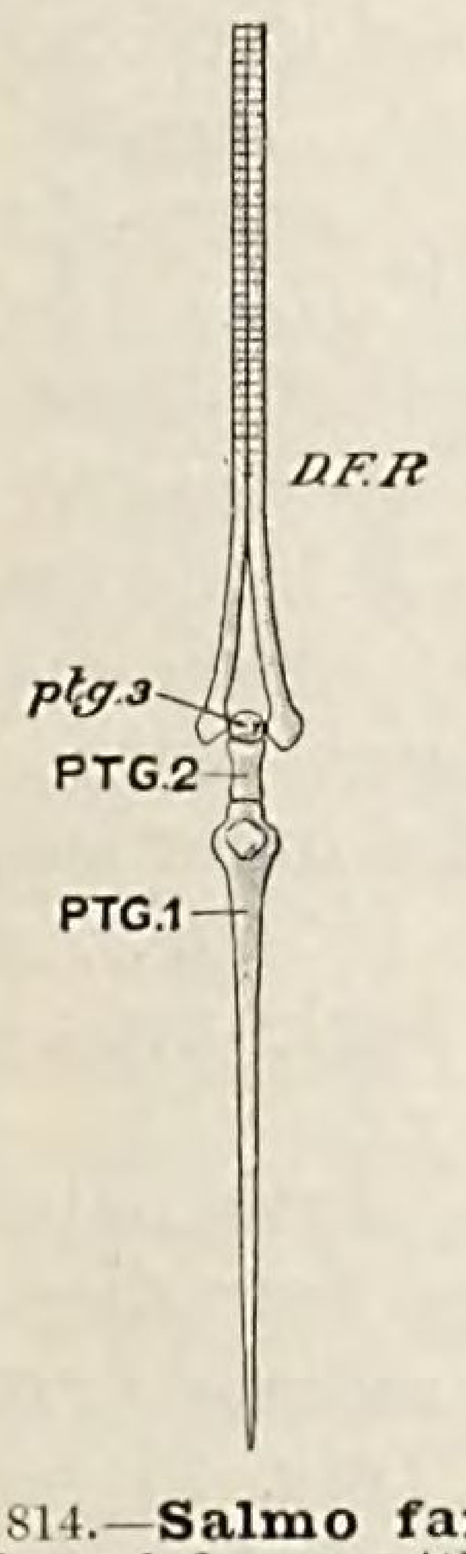


FIG. 814.—**Salmo fario.** A dermal fin-ray with its supports. *D.F.R.* dermal fin-ray; **PTG**.1, proximal pterygiophore (inter-spinous bone); **PTG** 2, middle pterygiophore; *ptg.3*, distal pterygiophore (cartilaginous).

the dermal rays (*D.F.R.*) are similarly seated on the broad hæmal arches of the posterior caudal vertebræ. The second dorsal or adipose fin has no bony support.

The shoulder girdle (Fig. 815), like the skull, consists of a *primary shoulder girdle*, homologous with that of a Dog-fish, and of several membrane bones. The primary shoulder-girdle in the young Fish is formed of distinct right and left bars of cartilage, which do not unite with one another ventrally. In the adult each bar is ossified by three bones, a *scapula* (SCP.) situated dorsally to the glenoid facets, and developed partly as a cartilage, partly as a membrane bone; a *coracoid* (COR.), situated ventrally to the glenoid facet, and a *mesocoracoid* (MS. COR.) situated above the coracoid and anterior to the scapula. Externally to these is found a very large membrane bone, the *clavicle* (*CL.*), extending downwards under the throat: its dorsal end is connected by means of a *supra-clavicle* (*S. CL.*) to a forked bone, the *post-temporal* (*P. TM.*), one branch of which articulates with the

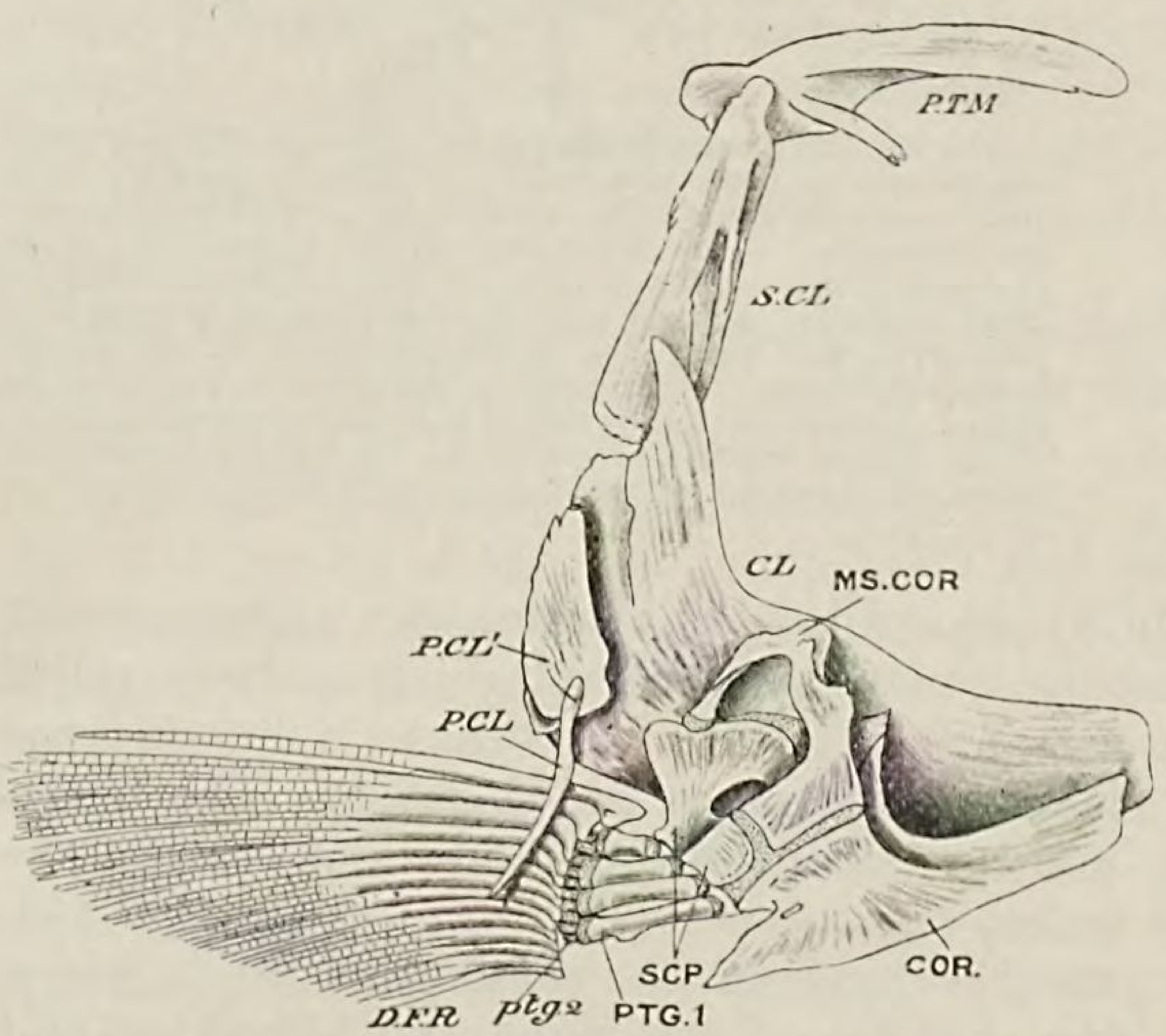


FIG. 815.—**Salmo fario.** Left half of shoulder-girdle and pectoral fin, from the inner surface. *CL.* clavicle; **COR.** coracoid; *D. F. R.* dermal fin-rays; **MS. COR.** meso-coracoid; *P. CL.*, *P. CL'.* post-clavicles; **PTG.1,** proximal; *ptg.2*, distal pterygiophores; *P. TM.* post-temporal; *S. CL.* supra-clavicle; **SCP.** scapula.

epiotic, the other with the pterotic process. To the inner surface of the clavicle are attached two flat scales of bone (*P. CL'.*), with a slender rod-like *post-clavicle* (*P.CL.*) passing backwards and downwards among the muscles.

The structure of the *pectoral fin* is very simple. Articulated to the posterior border of the scapula and coracoid are four dice-box shaped bones, the proximal pterygiophores or radials (PTG.1), followed by a row of small nodules of cartilage (*ptg.* 2) representing distal pterygiophores. The main body of the fin is supported by dermal fin-rays, which resemble those of the median fins, and have their forked ends seated upon the distal pterygiophores: the first ray, however, is larger than the rest, and articulates directly with the scapula.

There is no pelvic girdle, its place being taken by a large, flat, triangular bone, the *basi-pterygium* (Fig. 816, B. PTG.), probably representing fused proximal pterygiophores: to its posterior border are attached three partly ossified nodules, the distal pterygiophores (PTG.), and with these the dermal fin rays are articulated. The adipose lobe of the pelvic fin is supported by a small scale-like bone.

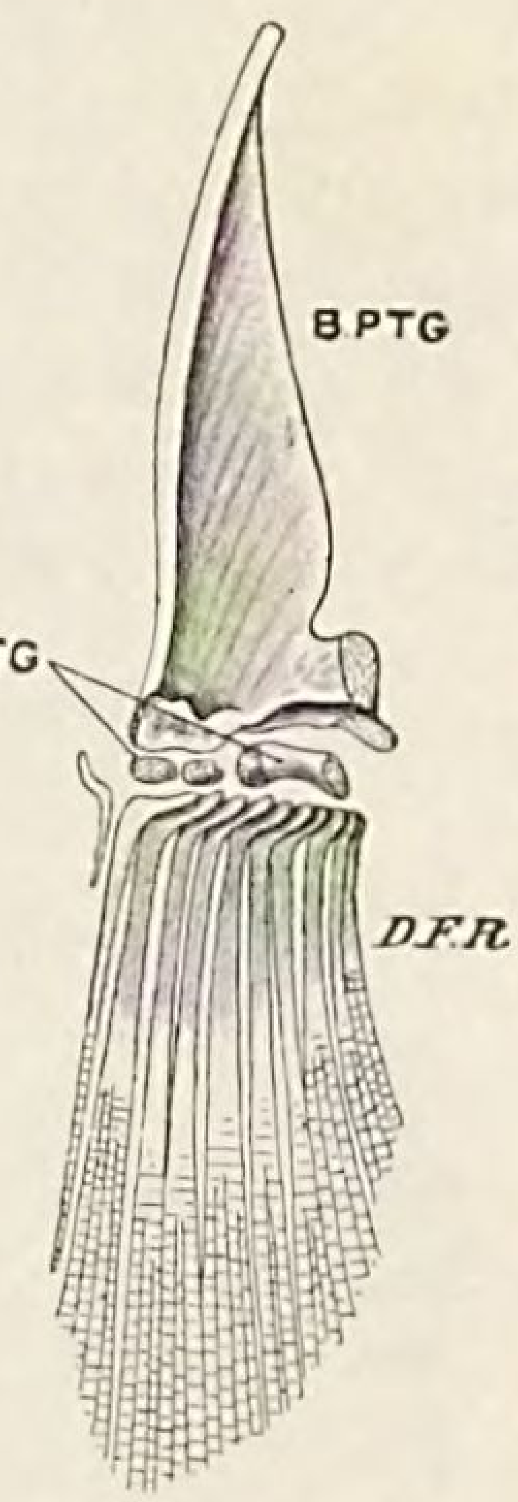


FIG. 816.—**Salmo fario.** Skeleton of left pelvic fin, dorsal aspect. **B. PTG.** basi-pterygium; *D. F. R.* dermal fin-rays; **PTG.** distal pterygiophores.

The **muscles** of the trunk and tail are arranged, as in the Dog-fish, in zigzag myomeres: there are small muscles for the fins, and the head has a complex musculature for the movement of the jaws, hyoid, operculum, and branchial arches.

The **cœlome** is divisible into a large *abdomen* (Fig. 817) containing the chief viscera, and a small *pericardial cavity*, situated below the branchial arches, and containing the heart.

Digestive Organs.—The *mouth* (Figs. 807 and 817) is very large, and has numerous small recurved, conical teeth, borne, as already mentioned, on the premaxillæ, maxillæ, palatines, vomer, dentaries, and basi-hyal. They obviously serve merely to prevent the escape of the slippery animals used as food and are of no use for either rending or chewing. The *pharynx* (*ph.*) is perforated on each side by four vertically elongated gill-slits, fringed by the bony tooth-like gill-rakers. Each gill-slit is V-shaped, the epi-hyal being bent upon the cerato-hyal so that the dorsal and ventral moieties of the branchial arches touch one another when the mouth is closed.

The pharynx leads by a short *gullet* (*gul.*) into a U-shaped *stomach* (*st.*), consisting of a wide cardiac and a narrow pyloric division: between the latter and the intestine is a ring-shaped pyloric valve. The *intestine* passes at first forwards as the *duodenum* (*du.*), then becomes bent upon itself (*int.*) and passes backwards, without convolution, to the anus (*an.*). Its posterior portion has the mucous membrane raised into prominent annular ridges which simulate a spiral valve.

The *liver* (*lr.*) is imperfectly divided into right and left lobes, and there is a large gall-bladder (*g. bl.*). Opening into the duodenum are about forty blind glandular tubes, the *pyloric cæca* (*py.c.*). There is a large *spleen* (*spl.*) attached by peritoneum to the fundus of the stomach. The stomach, duodenum, and pyloric cæca are surrounded by loose folds of peritoneum loaded with fat.

Lying below the kidneys and extending the whole length of the

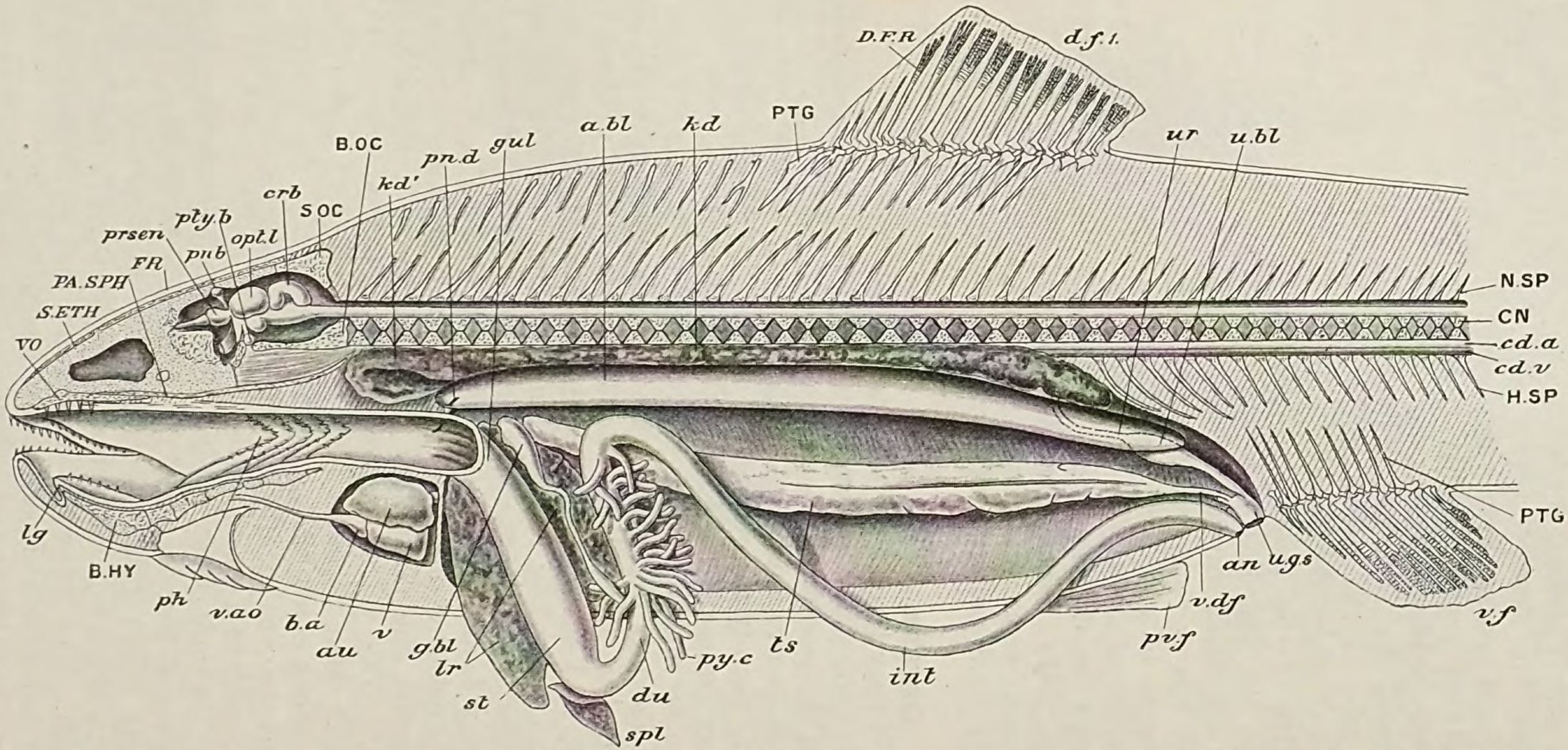


FIG. 817.—**Salmo fario.** Dissection from the left side. *a. bl.* air-bladder, opened; *an.* anus; *au.* auricle; *b. a.* bulbus aortæ; **B. HY.** basi-hyal **B. OC.** basi-occipital; *cd. a.* caudal artery; *cd. v.* caudal vein; **CN.** centrum; *crb.* cerebellum; *d. f. 1*, first dorsal fin; *D. F. R.* dermal fin-rays; *du.* duodenum; *FR.* frontal; *g. bl.* gall-bladder; *gul.* gullet; **H. SP.** hæmal spine; *int.* intestine; *kd.* kidney; *kd'.* degenerate portion of kidney; *lr.* liver; **N. SP.** neural spine; *opt. l.* optic lobes; *PA. SPH.* parasphenoid; *ph.* pharynx; *pn. b.* pineal body; *pn. d.* bristle passed into pneumatic duct; *prsen.* prosencephalon; *pty. b.* pituitary body; **PTG.** pterygiophores; *pv.f.* pelvic fin; *py. c.* pyloric cœca; *S. ETH.* supra-ethmoid; **S. OC.** supra-occipital; *spl.* spleen; *st.* stomach; *tg.* tongue; *ts.* testis; *u. bl.* urinary bladder; *u. g. s.* urino-genital sinus; *ur.* ureter; *v.* ventricle; *v. ao.* ventral aorta; *v. df.* vas deferens; *v. f.* ventral fin; *VO.* vomer.

abdominal cavity is the **air-bladder** (*a. bl.*), a thin-walled sac serving as an organ of flotation. Anteriorly its ventral wall presents a small aperture leading, by a short *pneumatic duct* (*pn.d.*), into the pharynx.

Respiratory Organs.—There are four pairs of *gills* each with a double row of branchial filaments united proximally but having their distal ends free: interbranchial septa are practically obsolete (see Fig. 726). The gills are borne on the first four branchial arches, the fifth arch bearing no gill. On the inner surface of the operculum is a comb-like body, the *pseudo-branchia*, formed of a single row of branchial filaments, and representing the vestigial gill (hemibranch) of the hyoid arch.

Circulatory Organs.—The *heart* (Fig. 817) consists of sinus venosus, auricle (*au.*), and ventricle (*v.*). There is no conus arteriosus, but the proximal end of the ventral aorta is dilated to form a *bulbus aortæ* (*b. a.*), a structure which differs from a conus in being part of the aorta and not of the heart; its walls do not contain striped muscle, and are not rhythmically contractile.

In accordance with the atrophy of the hyoid gill there is no afferent branchial artery to that arch, but a *hyoidean artery* springs from the ventral end of the first efferent branchial and passes to the pseudobranch. The right branch of the caudal vein is continued directly into the corresponding cardinal, the left breaks up in the kidney, forming a renal portal system. There are no lateral veins, but the blood from the paired fins is returned to the cardinals. The red blood corpuscles are, as in other fishes, oval nucleated discs.

Nervous System.—The brain (Fig. 818) is very different from that of Elasmobranchs, and is in many respects of a distinctly lower type. The *cerebellum* (*H. H.*) is very large, and bent upon itself. The *optic lobes* (*M. H.*) are also of great size, and corresponding with them on the ventral surface are large bean-shaped *lobi inferiores* (*U. L.*). The *diencephalon* is much reduced, and, indeed, is indicated dorsally only as the place of origin of the pineal body (*G. p.*): ventrally it is produced into the lobi inferiores with the infundibulum between them giving attachment to the pituitary body (*Hy. p.*). Hence, seen from above, the small undivided *prosencephalon* (*V. H.*) comes immediately in front of the mid-brain: it has a non-nervous roof or pallium (*Pall.*) and its floor is raised into prominent corpora striata (*B. G.*, *Bas. G.*). The *olfactory lobes* (*L. ol.*) are nearly as large as the corpora striata, and each contains a small cavity or rhinocœle in communication with the undivided prosocœle. Three transverse bands of fibres connect the right and left halves of the fore-brain, an *anterior commissure* joining the corpora striata, a *posterior commissure* situated just behind the origin of the pineal body, and an *inferior commissure* in front of the infundibulum. The *pineal body* (*b. p.*)

is rounded and placed at the end of a hollow stalk: a shorter offshoot of the roof of the diencephalon may perhaps represent a rudimentary pineal eye. Behind the pituitary body is a saccus

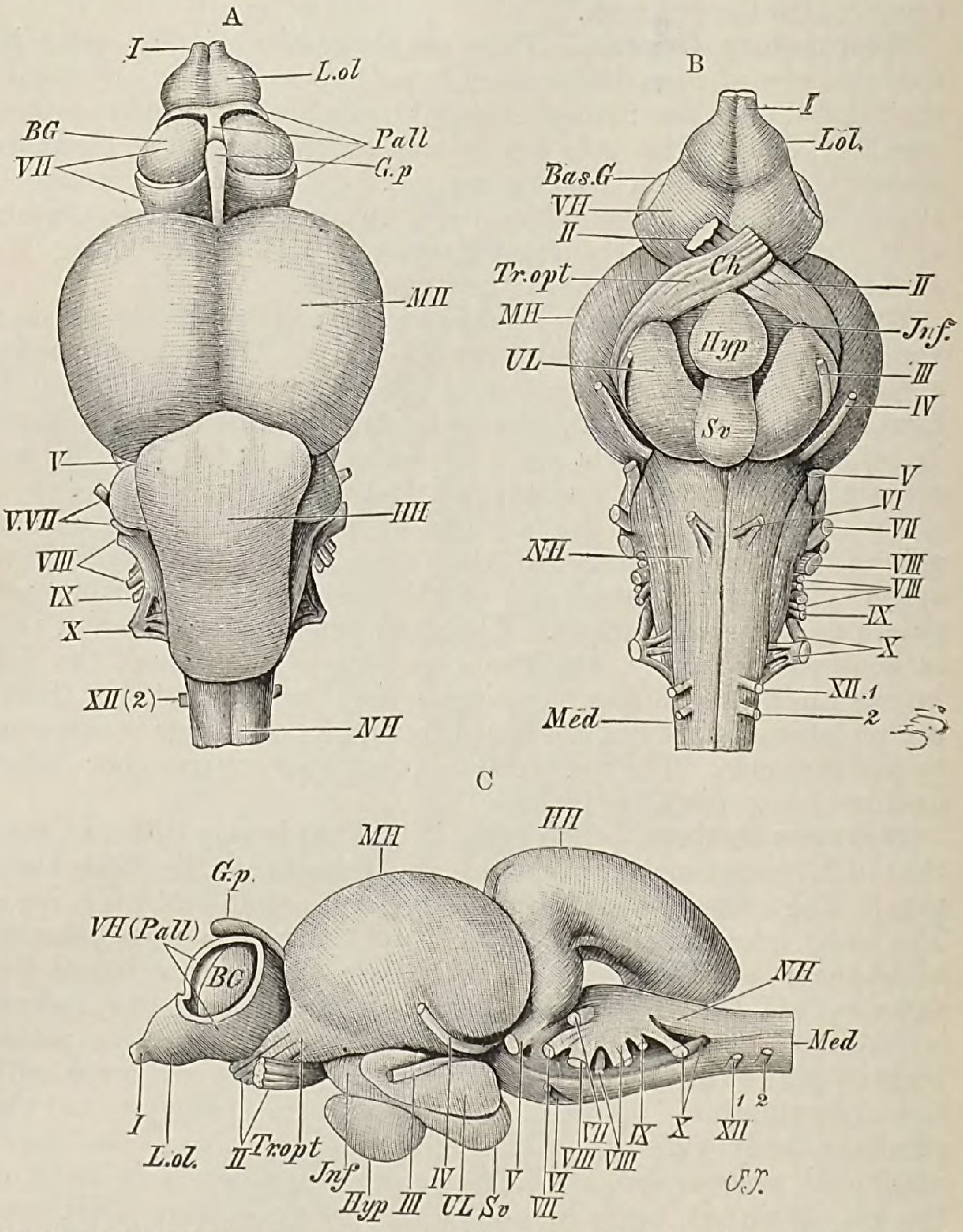


FIG. 818.—**Salmo fario.** Dorsal (A), ventral (B), and lateral (C) views of brain. *BG*, or *Bas G.* corpora striata; *ch*, crossing of optic nerves; *G. p*, pineal body; *HH*, cerebellum; *Hyp*, pituitary body; *Inf.* infundibulum; *L. ol.* olfactory lobes; *Med*, spinal cord; *MH*, optic lobes; *NH*, medulla oblongata; *Pall.* pallium; *Sv.* saccus vasculosus; *Tr. Opt.* optic tracts; *U, L*, lobi inferiores; *VH*, prosencephalon; *I—X*, cerebral nerves; *XII, 1*, first spinal (hypoglossal) nerve; *2*, second spinal nerve. (From Wiedersheim's *Vertebrata.*)

vasculosus (*s. v.*). The *optic nerves* do not form a chiasma, but simply cross one another or decussate (*Ch.*) on leaving the brain, the right nerve going to the left, and the left nerve to the right eye.

Sensory Organs.—The most distinctive feature of the *olfactory sac* is the possession of two small apertures, the anterior provided with a valve.

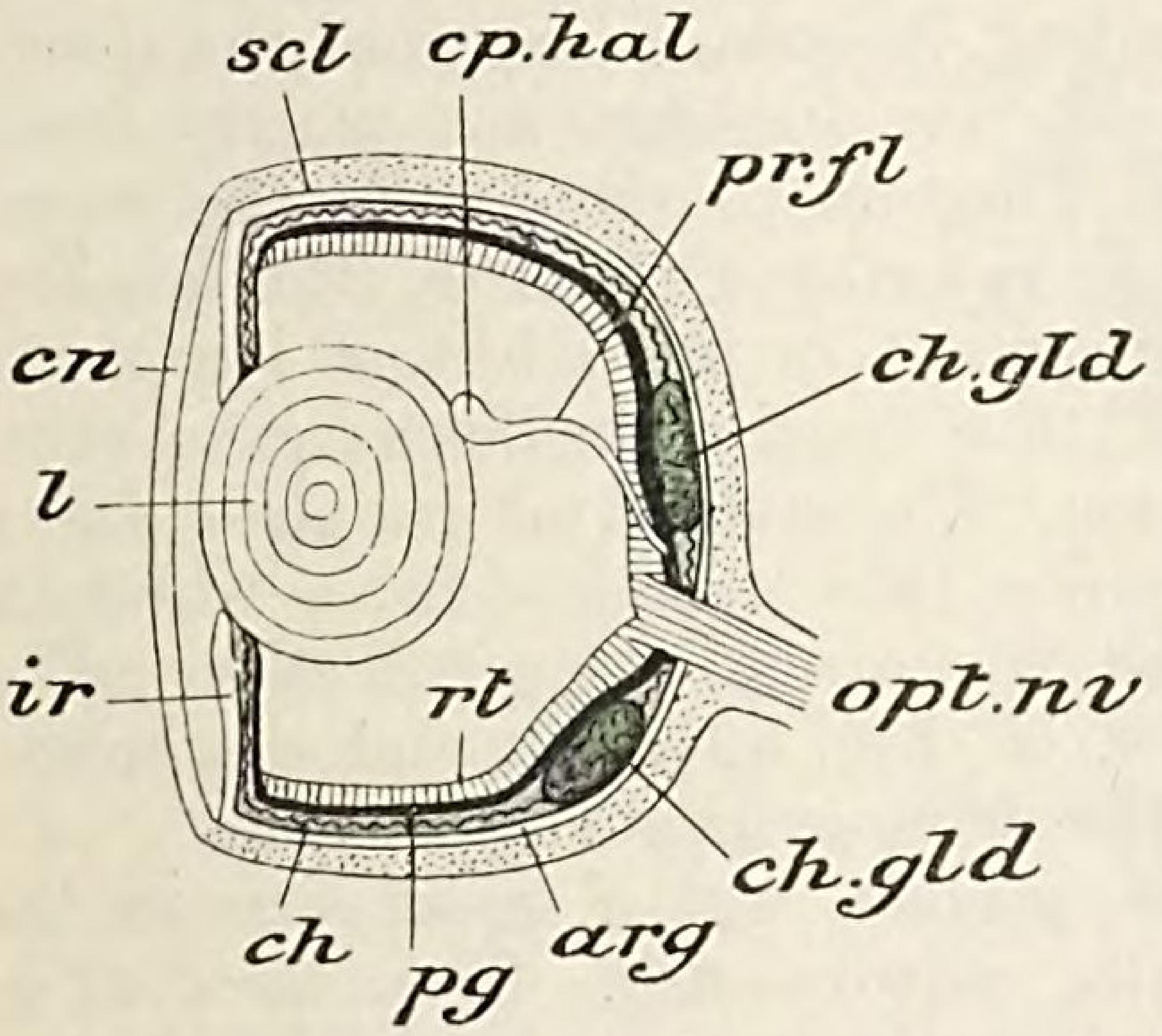


FIG. 819.—**Salmo fario.** Vertical section of eye (semi-diagrammatic). *arg.* argentea; *ch.* choroid; *ch. gld.* choroid gland; *cn.* cornea; *cp. hal.* campanula Halleri; *ir.* iris; *l.* lens; *opt. n.* optic nerve; *pg.* pigmentary layer; *pr. fl.* processus falciformis; *scl.* sclerotic (dotted).

The *eye* (Fig. 819) has a very flat *cornea* (*cn.*) with which the globular *lens* (*l.*) is almost in contact, so that the anterior chamber of the eye is extremely small. Between the cartilaginous *sclerotic* (*scl.*) and the vascular *choroid* (*ch.*) is a silvery layer or *argentea* (*arg.*) which owes its colour to minute crystals in the cells of which it is composed. In the posterior part of the eye, between the choroid and the argentea, is a thickened ring-shaped structure (*ch. gld.*) surrounding the optic nerve, and called the *choroid gland:* it is not glandular, but is a complex network of blood vessels or *rete mirabile.* It is supplied with blood by the efferent artery of the pseudobranch. Close to the entrance of the optic nerve a vascular fold of the choroid, the *falciform process* (*pr. gl.*), pierces the retina, and is continued to the back of the lens where it ends a knob, the *campanula Halleri* (*cp. hal.*), which contains smooth muscular fibres, and is probably concerned in accommodation by altering the curvature of the lens.

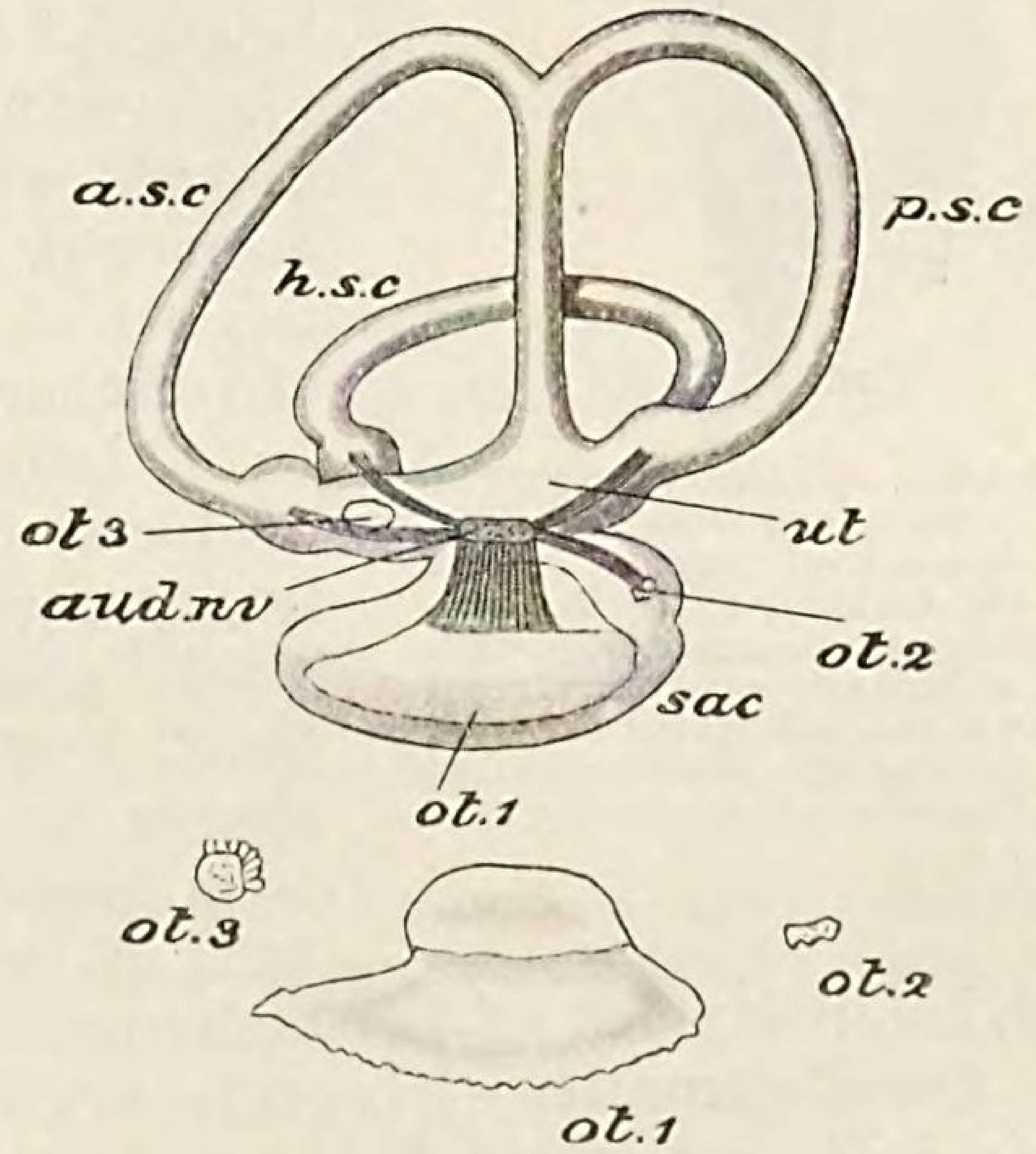


FIG. 820.—**Salmo fario.** The right auditory organ, from the inner side; the otoliths are shown separately below. *a. s. c.* anterior semicircular canal; *aud. nv.* auditory nerve; *h. s. c.* horizontal canal; *ot. 1—3*, otoliths; *p. s. c.* posterior canal; *sac.* sacculus; *ut.* utriculus.

The *auditory organ* (Fig. 820) is chiefly remarkable for the large size of the *otoliths* (*ot. 1–3*). They are three in number; one, called the *sagitta* (*ot. 1*), is fully 6 mm. in length, and almost fills the sacculus: another, the *asteriscus* (*ot. 2*), is a small granule lying in the lagena or rudimentary cochlea: the third (*ot. 3*)

is placed in the utriculus close to the ampullae of the anterior and horizontal canals.

Urino-genital Organs.—The *kidneys* (Fig. 817, *kd.*, and Fig. 821, *R.*) are of great size, extending the whole length of the dorsal wall of the abdomen, above the air bladder, and partly fused together in the middle line. They are derived from the mesonephros of the embryo. Their anterior ends (Fig. 817, *kd*, Fig. 821, *R*) are much dilated and consist in the adult of lymphatic tissue, thus ceasing to discharge a renal function. The *ureters* (mesonephric ducts, *ur.*) unite into a single tube, which is dilated to form a *urinary bladder* (Fig. 817, *u. bl.*, Fig. 821, *v.*), and discharges into the urino-genital sinus.

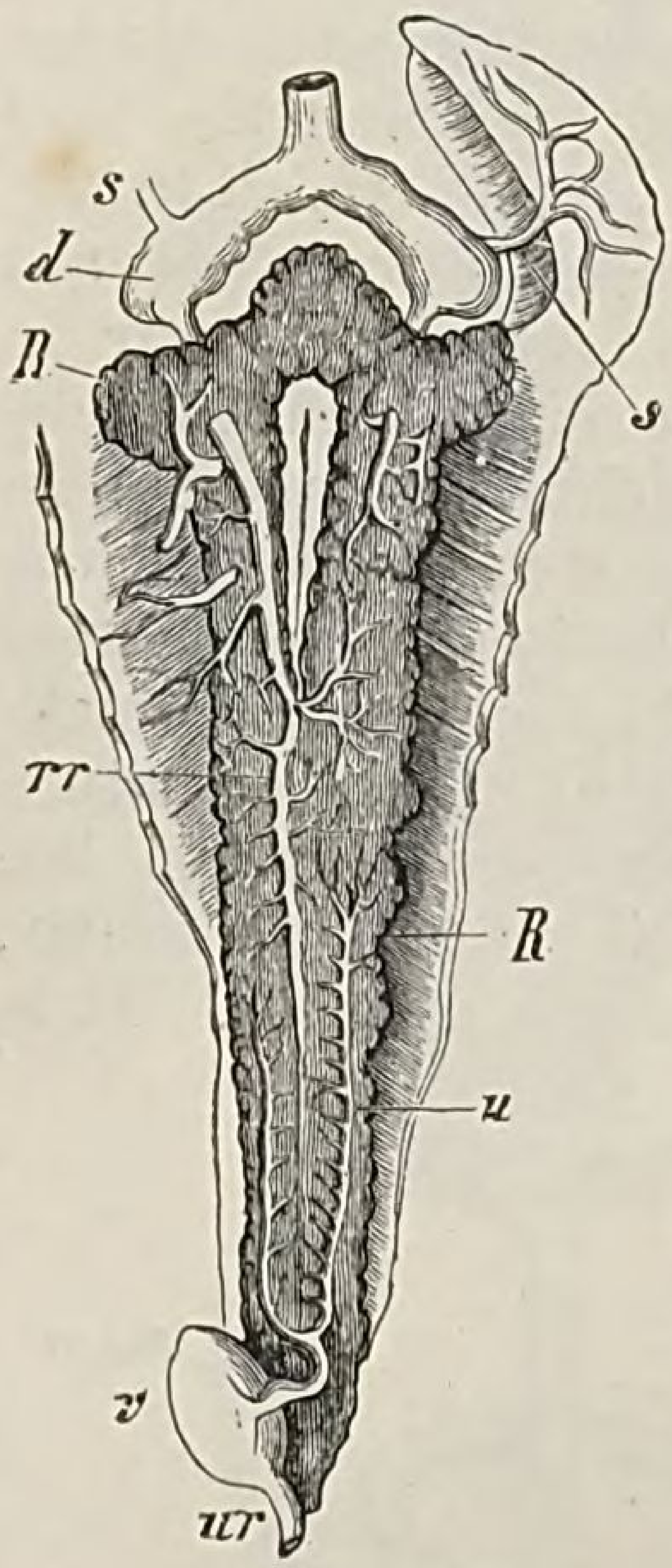


FIG. 821.—**Salmo fario.** The kidneys and adjacent parts. *d*, pre-caval vein; *R* (to the right) kidney; *R* (to the left), degenerate anterior portion of kidney; *rr*, efferent renal vein; *s*. subclavian vein; *u*, *ur*. ureter; *v*, bladder. (From Gegenbaur's *Comparative Anatomy*.)

The *gonads* are of great size in the sexually mature fish. The *testes* (Fig. 817, *ts.*) are long, smooth, pinkish, paired organs, extending the whole length of the abdominal cavity; each is continued posteriorly into a duct (*v. df.*) which opens into the urino-genital sinus, and the homology of which with the ducts of the primitive nephridial system is still uncertain. The ovaries are also of the full length of the abdominal cavity and are much wider than the testes: they are covered with peritoneum on their inner or mesial faces only, and the numerous ova, which are about 4 mm. in diameter, are discharged when ripe from their outer faces into the cœlome. There are no oviducts, but the anterior wall of the urinogenital sinus is pierced by a pair of *genital pores* through which the ova make their way to the exterior. There is reason for thinking that these pores are to be looked upon as degenerate oviducts, and in no way homologous with the abdominal pores of Elasmobranchs.

Development.—Impregnation is external, the male shedding his milt or seminal fluid on the newly laid eggs. The ovum is covered by a thick membrane, the *zona radiata*, perforated by an aperture, the *micropyle*, through which the sperms find access: it is formed of a superficial layer of protoplasm surrounding a mass of transparent fluid yolk of a pale yellow colour. At one pole the protoplasm accumulates to form an elevated area or *germinal disc*, in which segmentation takes place (Fig. 822, *A*, *B*) in

much the same way as in Elasmobranchs, except that, owing to the smaller proportion of yolk, the resulting blastoderm (*bl.*) and the embryo formed therefrom are proportionally much larger, and the yolk sac (*y. s.*) correspondingly smaller than in the two previous classes. Epiboly takes place as in Elasmobranchs, the blastoderm gradually growing round and enclosing the yolk (*C–F*). The embryo (*emb.*) arises as an elevation growing forwards from the thickened edge of the blastoderm, and, as it increases in length, appears as a clear colourless band (H, *emb.*) winding round the yellow yolk, and kept in close contact with it by the enclosing zona radiata. There is no open medullary groove, the nervous system being formed, as in Cyclostomes, from a fold of ectoderm, the walls of which are in apposition. Gradually the head and tail become free from the yolk, and at the time of hatching the yolk-sac (I, *y. s.*) is a shoe-shaped body sessile upon the ventral surface of the transparent embryo.

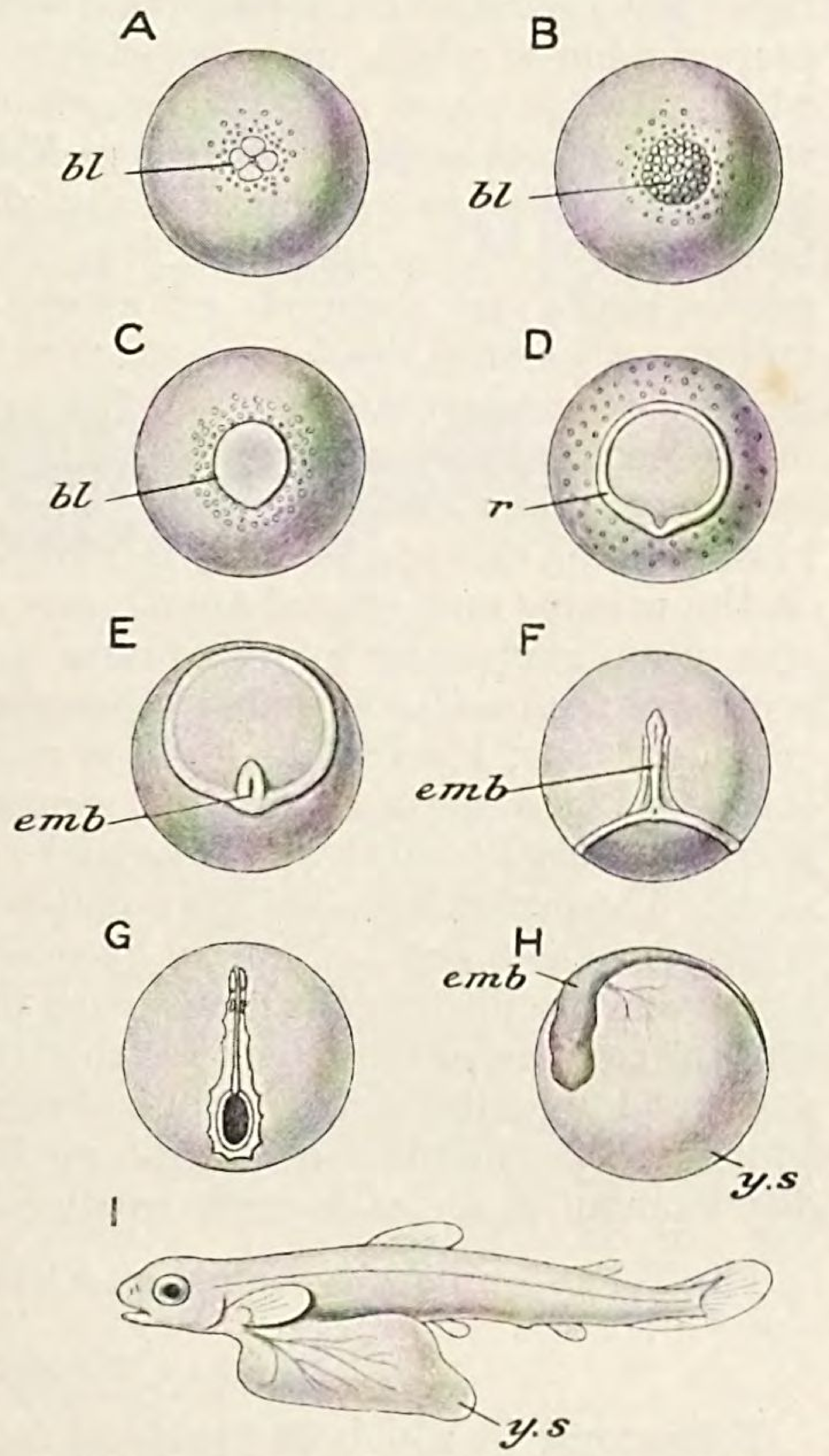


FIG. 822.—Nine stages in the development of **Salmo fario**. A—H, before hatching; I, shortly after hatching. *bl.* blastoderm; *emb.* embryo; *r*, thickened edge of blastoderm; *ys.* yolk-sac. (A—G after Henneguy.)

2.—Distinctive Characters and Classification.

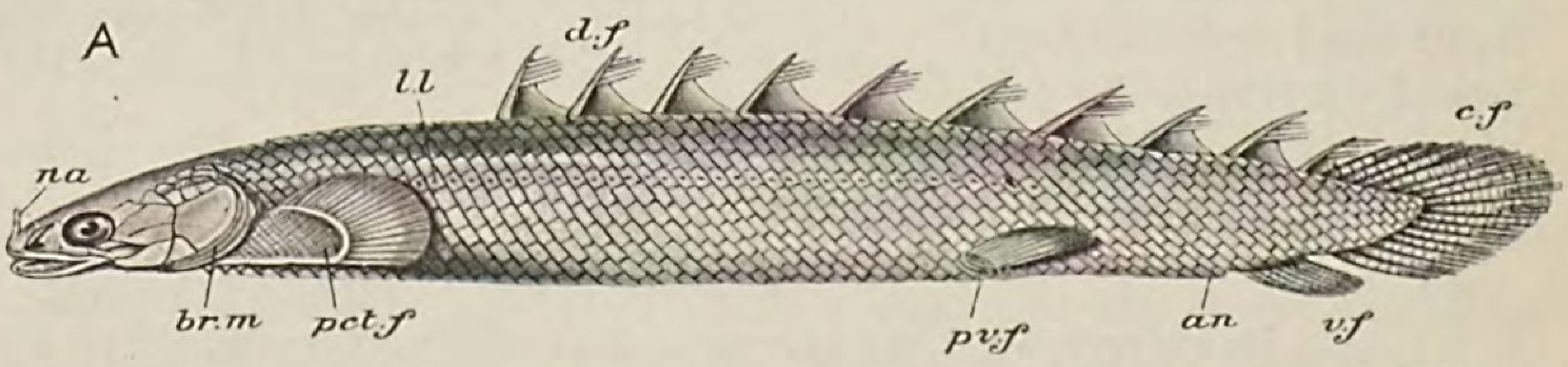
The Teleostomi are Pisces in which the primary cranium is always complicated by the addition of membrane bones, of which a pair of parietals and one of frontals above, and unpaired vomer and parasphenoid below, are the most constant. The chondrocranium is always more or less ossified by cartilage bones, and the upper and lower jaws are both bounded by membrane bones. The

jaws are connected with the cranium through the intermediation of a hyomandibular, which is probably not homologous with the similarly named element of Elasmobranchs. The dermal fin-rays are formed of membrane bone, and are supported by pterygiophores which may be either cartilaginous or bony, but which always show a great reduction in number as compared with the homologous structures in Elasmobranchs. The primary shoulder-girdle is complicated by the addition of membrane bones, of which a large clavicle is the most constant. The pelvic girdle is vestigial or absent. The pelvic fins usually undergo a forward displacement, their position being either *abdominal, i.e.* between the anus and the pectoral region, or *thoracic, i.e.* in the pectoral region, or *jugular, i.e.* under the throat. A dermal exoskeleton is usually present. The intestine may or may not have a spiral valve; the anus is distinct from, and placed in front of, the urinary and genital apertures. The gills are covered by an operculum supported by membrane bones, and the interbranchial septa are reduced or absent, so that the gill-filaments are partially or wholly free; the hyoidean gill is reduced or absent. The conus arteriosus is sometimes present, sometimes absent; when absent there is a large bulbus aortæ formed as a dilatation of the ventral aorta. The prosencephalon has a non-nervous roof; the optic nerves either form a chiasma or simply decussate. The ova are small; the gonoducts are either continuous with the gonads, or open anteriorly into the cœlome, or are absent: in the latter case the sexual products pass out by genital pores; true abdominal pores may be present in addition. Segmentation of the egg is either entire or discoidal; development is sometimes accompanied by a metamorphosis.

The Teleostomi are classified as follows:—

Order 1.—Crossopterygii.

Teleostomi in which the pectoral fin consists of a rounded basal lobe supported by endoskeletal structures and fringed by dermal



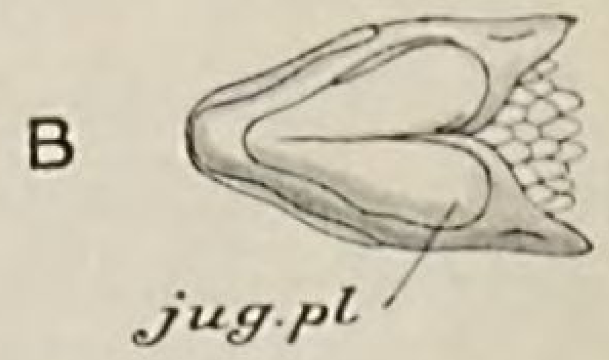


Fig. 823.—**Polypterus bichir.** A, entire animal; B, ventral view of throat. *an.* anus; *br. m.* branchiostegal membrane; *c. f.* caudal fin; *d. f.* dorsal finlets; *jug. pl.* jugular plates; *na.* nostril; *pct. f.* pectoral fin; *pv. f.* pelvic fin; *v. f.* ventral fin. (After Cuvier.)

rays. There are no branchiostegal rays. The vertebral column is well ossified, and the caudal fin is diphycercal. The pelvic fins are

abdominal. A spiral valve and a conus arteriosus are present, and the optic nerves form a chiasma.

The only existing members of this order are *Polypterus bichir* (Fig. 823), from the Upper Nile, and *Calamoichthys calabaricus* from Old Calabar.

ORDER 2.—CHONDROSTEI.

Teleostomi in which the paired fins have no basal lobe, but their whole free portion is supported by dermal rays. There are few

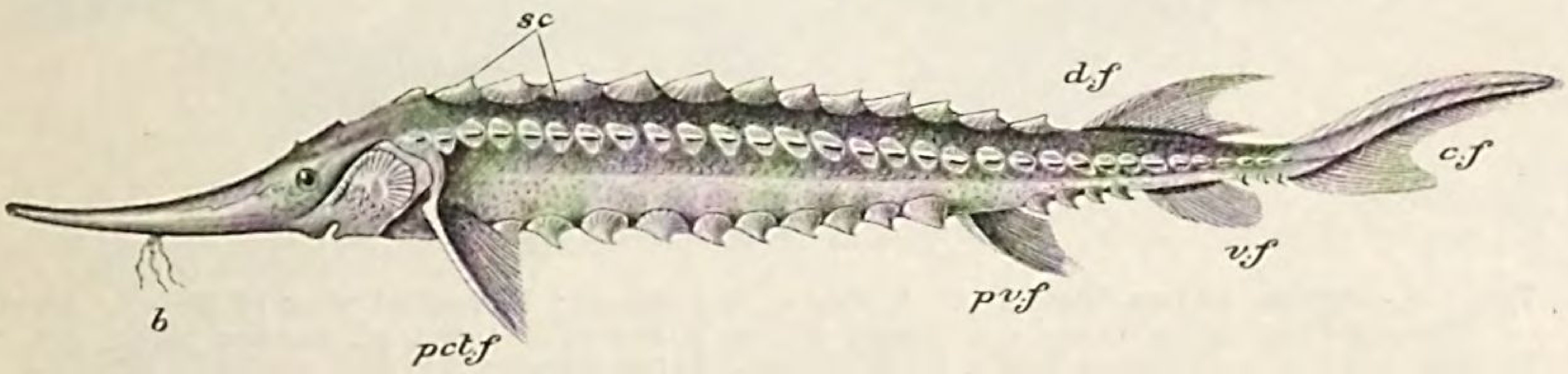


FIG. 824.—**Acipenser ruthenus** (Sturgeon). *b.* barbels; *c. f.* caudal fin; *d. f.* dorsal fin *pct. f.* pectoral fin; *pv. f.* pelvic fin; *sc.* scutes; *v. f.* ventral fin. (After Cuvier.)

cartilage bones in the skull, and the primary shoulder-girdle is unossified. The vertebral column consists of a persistent notochord with cartilaginous arches, and its anterior end is fused with the cranium. Branchiostegal rays are few or absent. The tail is heterocercal. The pelvic fins are abdominal. A spiral valve, conus arteriosus, and optic chiasma are present.

This order includes the Sturgeons (*Acipenser* and *Scaphirhynchus*, Fig. 824), found in the rivers of Europe, Asia, and North America; the curious spoon-billed *Polyodon*, from the Mississippi; and *Psephurus* from the rivers of China.

ORDER 3.—HOLOSTEI.

Teleostomi in which the paired fins have no basal lobe. The chondrocranium is well ossified by cartilage bones and invested by

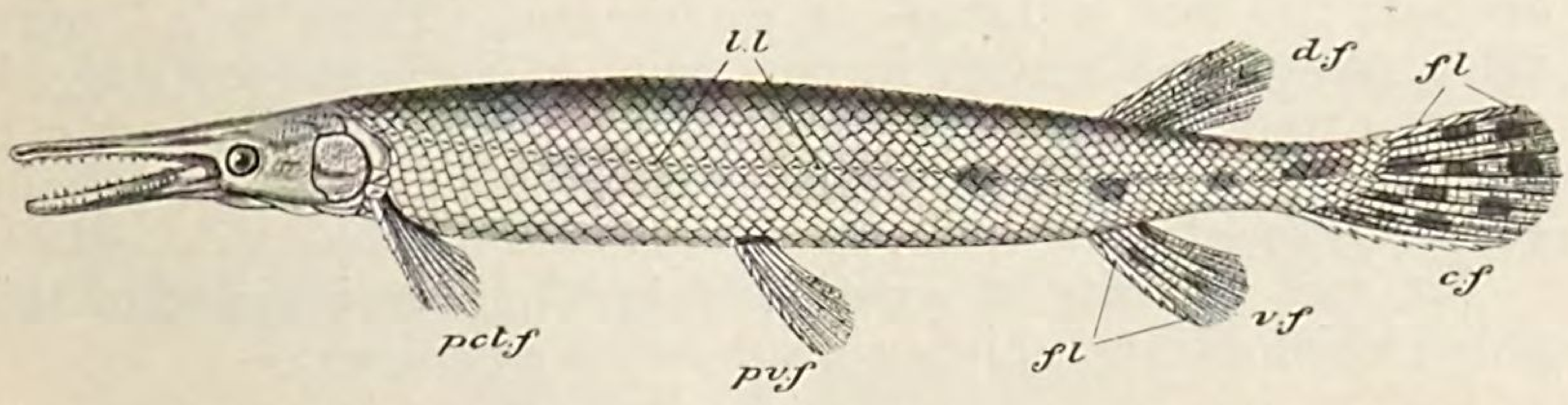


FIG. 825.—**Lepidosteus platystomus** (Bony Pike). *c.* . caudal fin; *d. f.* dorsal fin; *fl.* fulcra; *l. l.* lateral line; *pct. f.* pectoral fin; *pv. f.* pelvic fin; *v. f.* ventral fin. (After Cuvier.)

membrane bones: branchiostegal rays are present. The vertebral column consists of bony vertebræ, and the tail is heterocercal or

nearly homocercal. The pelvic fins are abdominal. A reduced spiral valve, a conus arteriosus, and an optic chiasma are present.

This order includes the Gar-pike or Bony Pike (*Lepidosteus*, Fig. 825), from the fresh waters of North and Central America and

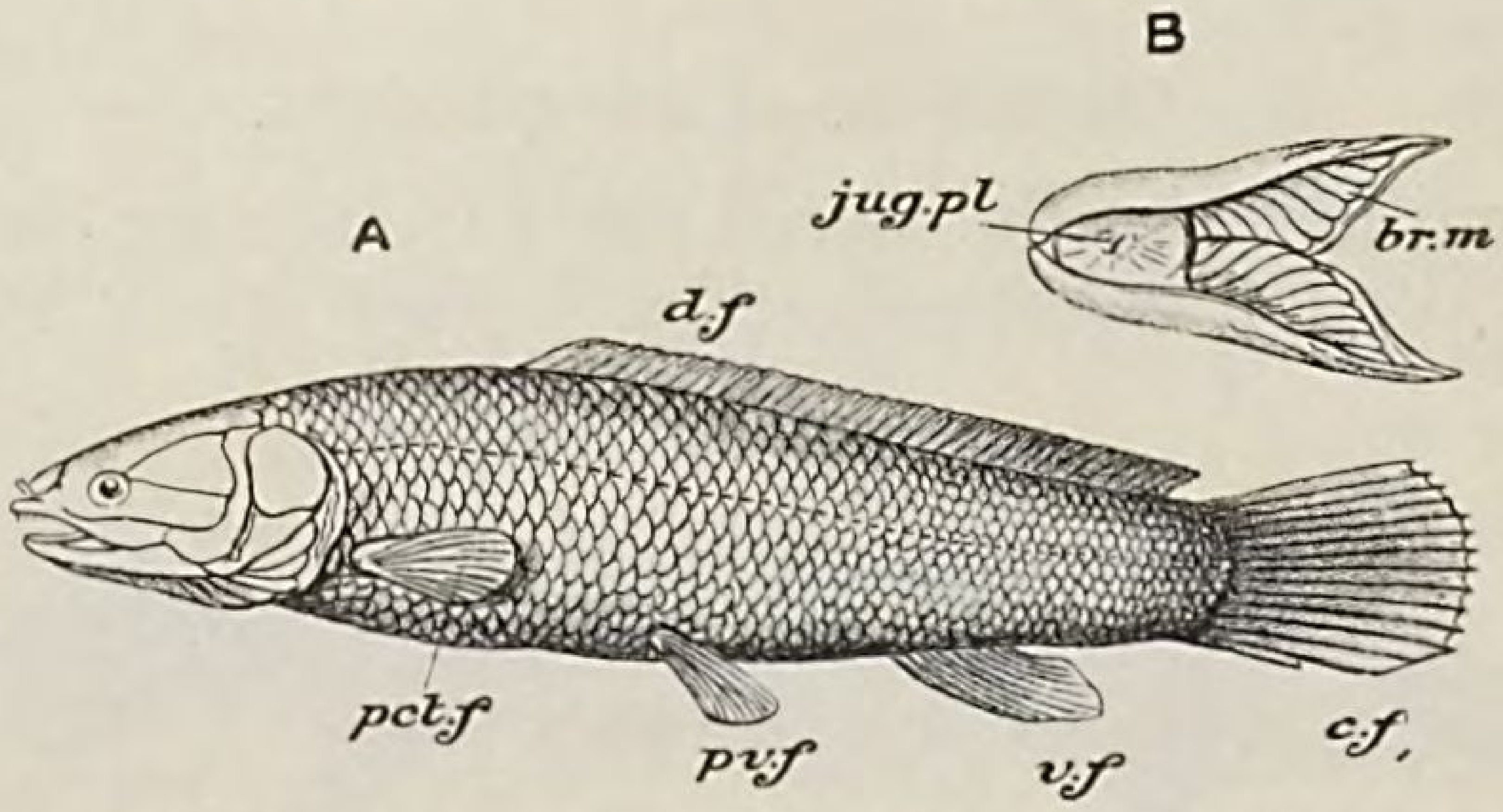


FIG. 826.—**Amia calva** (Bow-fin). A, the entire animal; B, ventral view of throat. *br. m.* branchiostegal membrane; *c. f.* caudal fin; *d. f.* dorsal fin; *jug. pl.* jugular plate; *pct. f.* pectoral fin; *pv. f.* pelvic fin; *v. f.* ventral fin. (After Günther.)

Cuba, and the Bow-fin or Mud-fish (*Amia calva*, Fig. 826), from the rivers of the United States.

Orders 1—3 are frequently grouped together as the sub-class *Ganoidei*, and, although such a group is an artificial one, it will often be convenient to refer to these fishes as "Ganoids." They are all small and numerically insignificant groups at the present day, but formed the whole of the Teleostomian fauna in the Palæozoic and the greater part of the Mesozoic epoch (*vide infra*).

ORDER 4.—TELEOSTEI.

Teleostomi in which the paired fins have no basal lobe. The skull is well ossified both by cartilage and membrane bones: branchiostegal rays are present. The vertebral column is well ossified: the tail is homo- or diphycercal. There is no spiral valve except as a vestige in one genus. The conus arteriosus is absent except as a vestige in one genus: a large bulbus aortæ is present. The optic nerves never form a chiasma and usually simply decussate.

The vast majority of existing Teleostomi are included in this order, which is divided into six sub-orders as follows:—

Sub-order a.—Physostomi.

Teleostei in which the air-bladder, when present, has an open pneumatic duct. All the fin-rays are jointed, and the pelvic fins, when present, are abdominal in position.

Including the Cat-fishes or Siluroids (Fig. 827), Carp, Gudgeon,

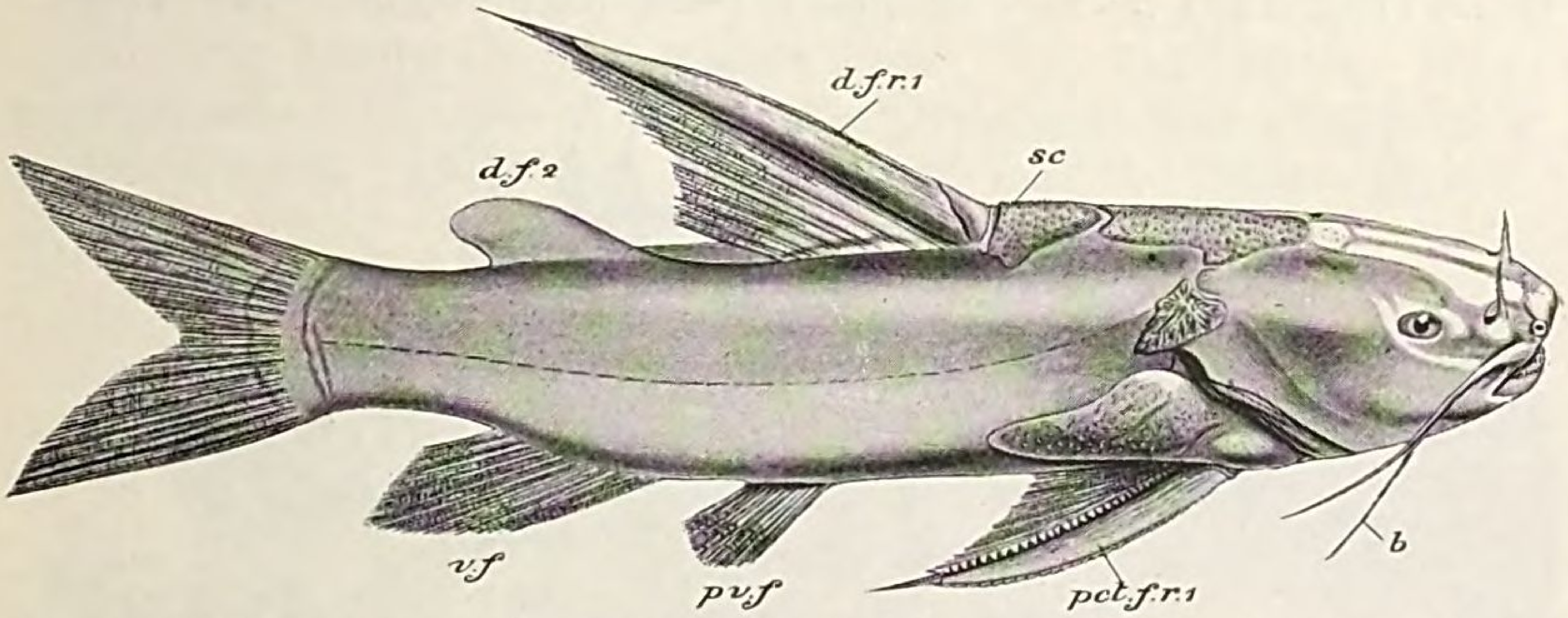


FIG. 827.—**Rita buchanani,** one of the Siluroids. *b.* barbel; *d. j. r. 1*, first dorsal fin-ray; *d. f. 2*, adipose fin; *pct. f. r. 1*, first pectoral fin-ray; *pv. f.* pelvic fin; *v. f.* ventral fin. (After Day.)

Loach, Pike, Salmon and Trout (Fig. 806), Smelt, Grayling, Herring, Anchovy, Eels, &c.

Sub-order b.—Anacanthini.

Teleostei in which the air-bladder, when present, has, except in one species, no pneumatic duct. The rays of the unpaired and of the pelvic fins are all jointed, and the pelvic fins are either thoracic or jugular. Including the Cod (Fig. 828), Haddock, Whiting,

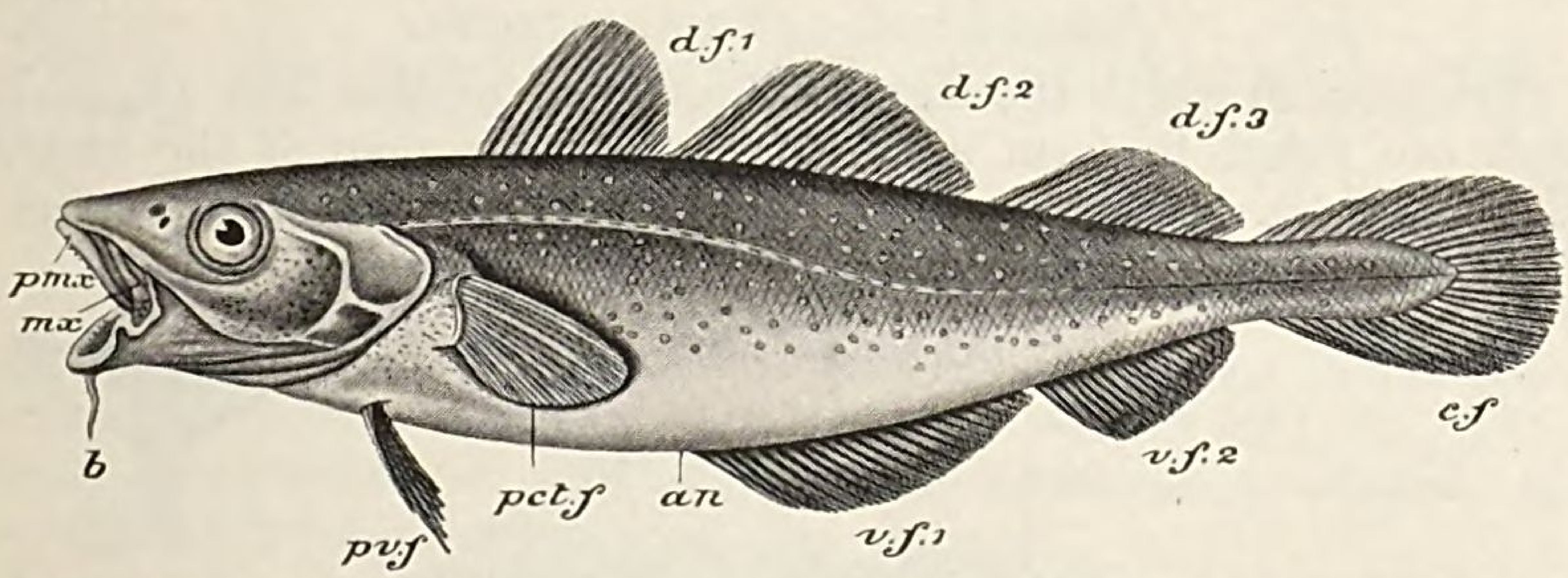


FIG. 828.—**Gadus morrhua** (Cod). *an.* anus; *c. f.* caudal fin; *d. . 1—3*, dorsal fins; *mx* maxilla; *pct. f.* pectoral fin; *pmx.* pre-maxilla; *vv. f.* pelvic fin; *v. f. 1* and *2*, ventral fins. (After Cuvier.)

Hake, Ling, and the Pleuronectidæ or Flat-fishes (Fig. 833), such as the Sole, Flounder, Turbot, &c.

Sub-order c.—Acanthopteri.

Teleostei in which the air-bladder, when present, has no pneumatic duct. More or fewer of the rays of the dorsal, ventral, and pelvic fins are unjointed and have the form of strong spines. The right and left bars of the fifth branchial arch are usually not fused

This immense group includes the greater number of marine fishes (Fig. 829), as well as many fresh-water forms: the Perch,

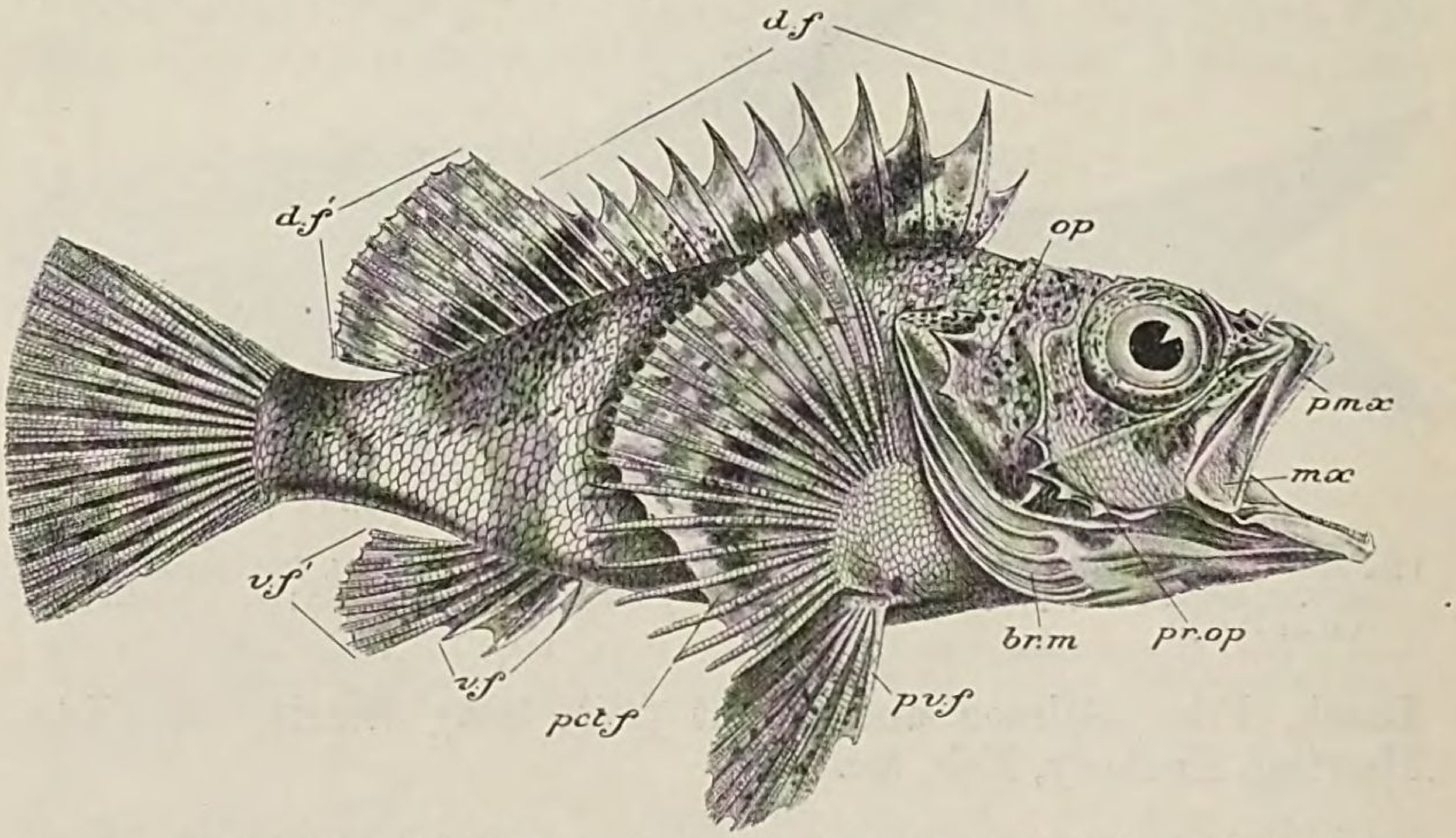


FIG. 829.—**Sebastes percoides.** *br. m.* branchiostegal membrane; *d. f.* spiny portion of dorsal fin; *d. f.'* soft portion; *mx.* maxilla; *op.* opercular; *pct. f.* pectoral fin; *p.mx.* pre-maxilla; *pr. op.* pre-opercular; *pv. f.* pelvic fin; *v. f.* spiny portion of ventral fin; *v. f.'* soft portion. (After Richardson.)

Stickleback, Sea-bream, Mullet, Mackerel, and Gurnard may be specially mentioned.

Sub-order d.—Pharyngognathi.

Teleostei in which the right and left bars of the fifth branchial arch are fused to form a single bone in the floor of the mouth (Fig. 830, B). The remaining characters are as in Acanthopteri.

Including the Wrasses (Fig. 830) and their allies.

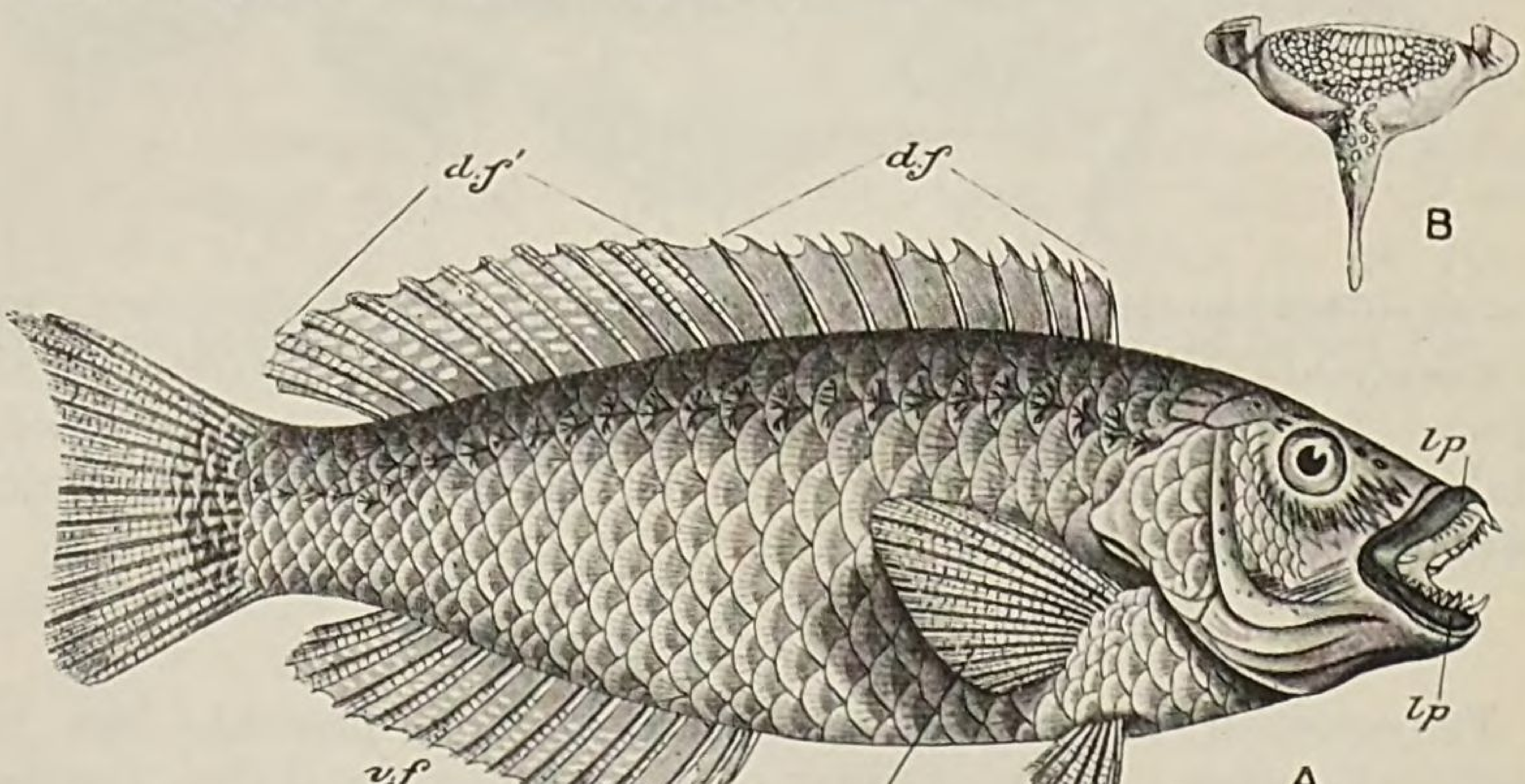


FIG. 830.—**Labrichthys psittacula** (Wrasse). *d. f.* hard dorsal; *d. f.'* soft dorsal; *lp.* lips; *pct. f.* pectoral fin; *pv. f.* pelvic fin; *v. f.* ventral fin. B, inferior pharyngeal bone of Labrichthys. (A, after Richardson; B, after Owen.)

Sub-order e.—Plectognathi.

Teleostei having no pneumatic duct. The exoskeleton, when present, takes the form of bony plates or spines. The gill-opening is very narrow. The mouth is very small, and the premaxilla and

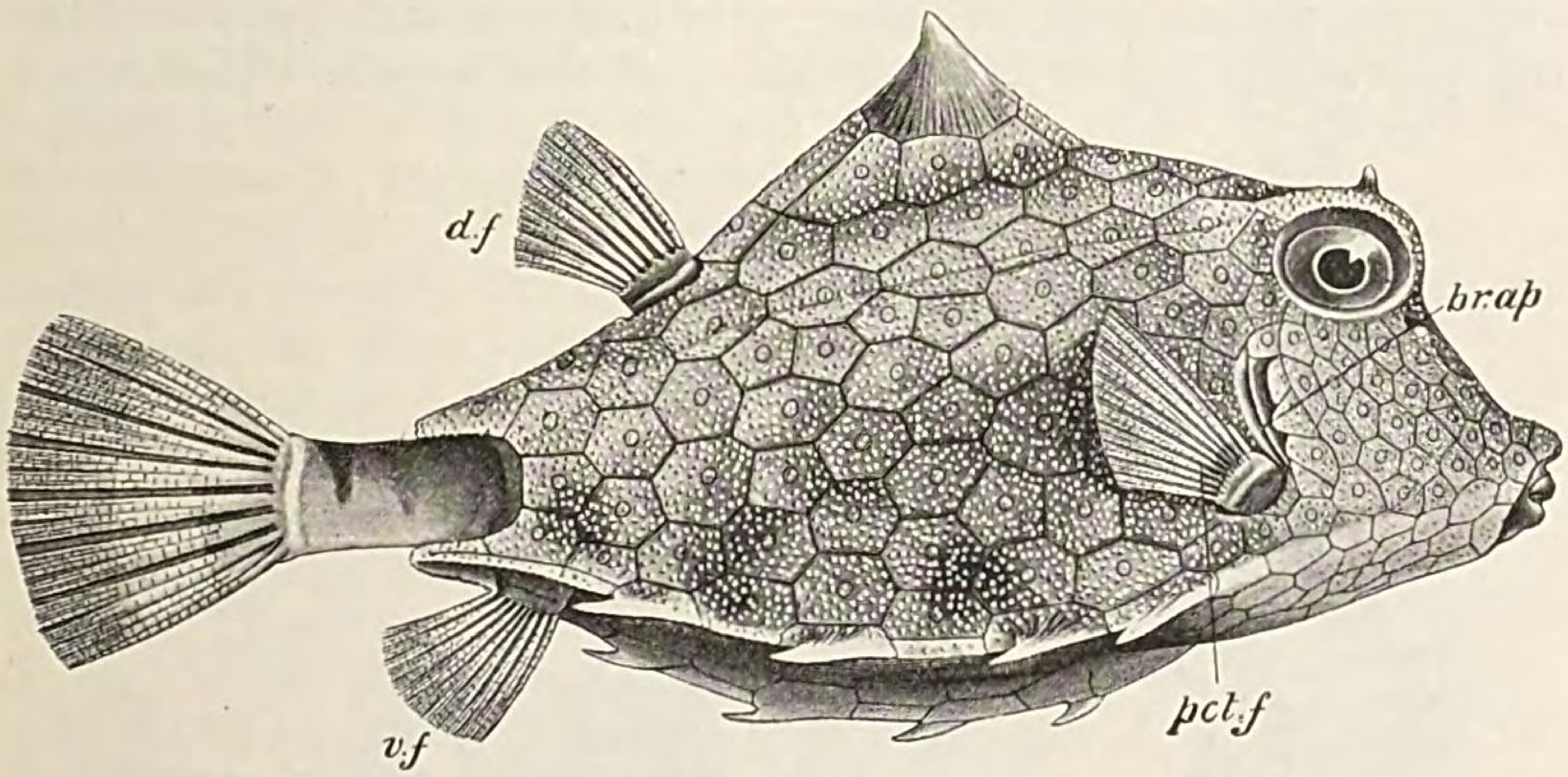


FIG. 831.—**Ostracion** (Coffer-fish). *br. ap.* branchial aperture; *d.f.* dorsal fin; *pct.f.* pectoral fin; *v. f.* ventral fin. (After Day.)

maxilla are united. The pelvic fins are absent or represented by spines.

This is a small sub-order, including the File-fishes, Globe-fishes, Sun-fishes and Coffer-fishes (Fig. 831).

Sub-order f.—Lophobranchii.

Teleostei having no pneumatic duct. The gills are not comb-like, but have their filaments arranged in tufts (Fig. 832, B). The branchial aperture is very small. The exoskeleton consists of bony plates arranged segmentally.

This is also a very small sub-order, including only the Sea-horses (Fig. 832), Pipe-fishes and their allies.

Sub-orders *b—f* are frequently grouped together as *Physoclisti*, distinguished from Physostomi by the closed air-bladder.

Systematic Position of the Example.

Salmo fario is one of several species of the genus *Salmo*, belonging to the family *Salmonidæ*, of the sub-order *Physostomi* and the order *Teleostei.*

The absence of a spiral valve and of a conus arteriosus, the presence of a bulbus aortæ, and the decussation of the optic nerves indicate its position among the Teleostei. It belongs to the Physostomi in virtue of possessing a pneumatic duct, none but jointed fin-rays, and abdominal ventral fins. The characters which place it among the Salmonidæ are the presence of an adipose fin and of pseudobranchiæ, the absence of oviducts, and the fact that the premaxilla enters into the gape of the mouth. The genus

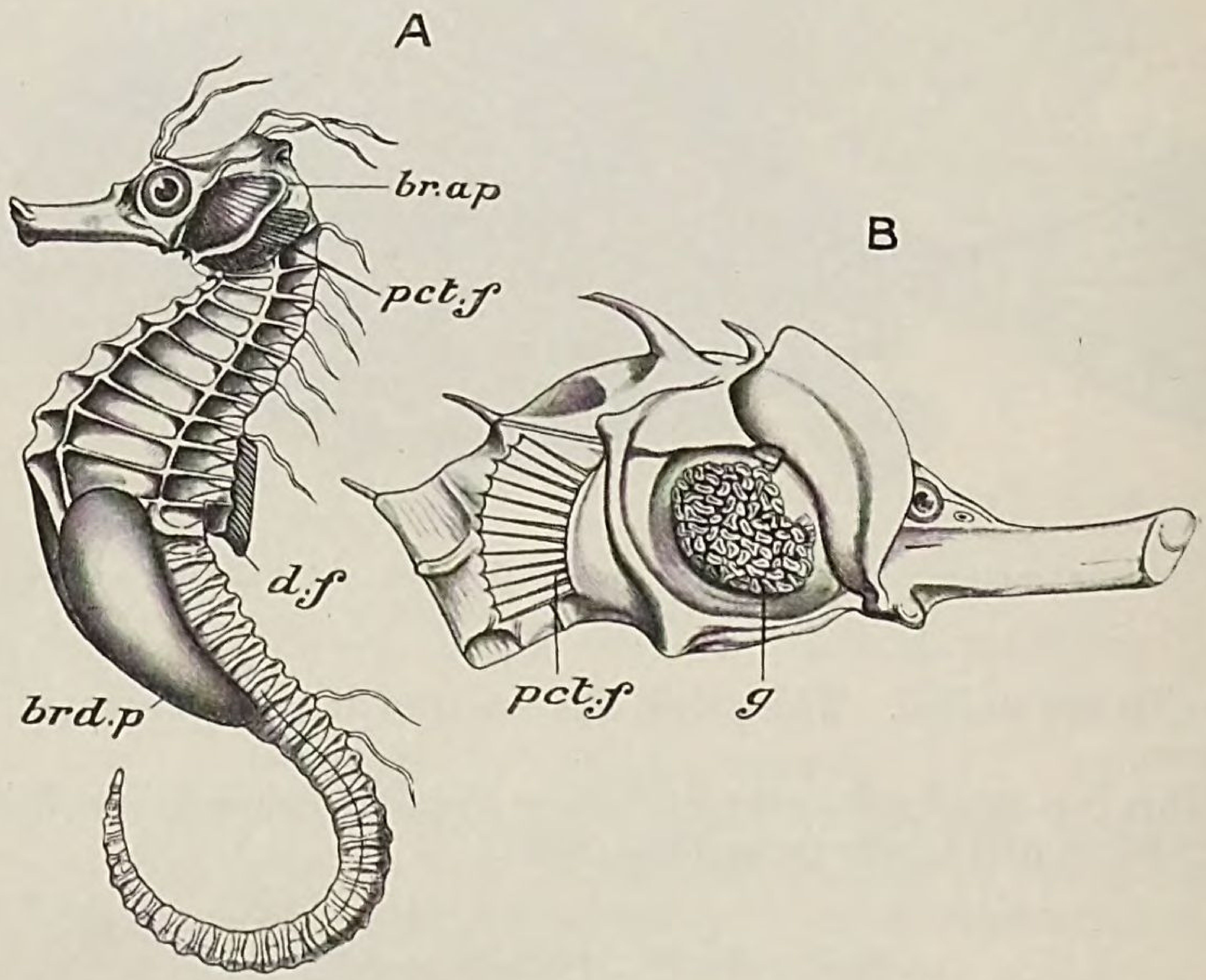


FIG. 832.—**Hippocampus** (Sea-horse). In B the operculum is removed to show the gills. *br. ap.* branchial aperture; *brd. p.* brood-pouch; *d. f.* dorsal fin; *g.* gills; *pct. f.* pectoral fin. (From Claus and Günther.)

Salmo is distinguished by its small scales, well-developed conical teeth, absent on the pterygoids, a short ventral fin with fewer than fourteen rays, numerous pyloric appendages, and comparatively large ova. The distinctive characters of the various species of Salmo depend upon comparatively minute points, such as the relative proportions of various parts, and are often difficult of determination owing to individual variations correlated with different environments. In *S. fario* the posterior margin of the operculum is evenly curved, the maxilla is longer than the snout, and the vomerine teeth are in a double series and persist throughout life.

3. General Organisation.

External Form.—The typical form of the Teleostomi is very fairly represented by that of the Trout (Fig. 806)—a long, compressed body, nearly half of which is formed by the tail, pointed anterior and posterior ends, a large vertical tail-fin, a head of moderate size, and a terminal mouth. Such a form is eminently fitted for rapid progression through the water. But from this characteristic fish-form there are many striking deviations. The body may be greatly elongated and almost cylindrical, as in the Eels; or of great length and strongly flattened from side to side, as in the Ribbon-fishes; or the head may be of immense proportional size and strongly depressed, as in certain shore-fishes, such as the Fishing-frog; or, as in the beautiful Reef-fishes, the whole body may be as high as it is long. The mouth sometimes has a ventral position, as in Elasmobranchs, with the snout prolonged over it. This is the case, for example, in the Sturgeons (Fig. 824); in the allied Polyodon the snout takes the form of a horizontally flattened shovel-like structure, about one-fourth the length of the body. On the other hand, in the ground-feeding "Star-gazers" and some other Acanthopteri the lower jaw is underhung like that of a bull-dog, and the mouth becomes dorsal in position. A *beak* may be produced by the prolongation of the upper jaw, as in the Sword-fish, or of the lower jaw, as in the Half-beak or Gar-fish, or of both jaws, as in the Bony-Pike (Fig. 825). Such a projection is not to be confounded with the snout of the Sturgeon or Polyodon, being formed by the elongation of the bones of the jaws (premaxilla, maxilla, dentary, &c.), whereas in the two Chondrostean forms referred to it is the anterior region of the cranium which is prolonged. Still another form of "snout" is produced in many Teleostei by the great mobility of the jaws, allowing of their protrusion in the form of a short tube. In the Wrasses or "lip-fishes" the mouth is bounded by fleshy lips (Fig. 830, *lp.*).

Tactile processes or *barbels* sometimes arise from the head; the most familiar example is that on the chin of the Cod and Haddock (Figs. 824 and 828, *b.*). An *operculum* is always present, and is supported by a variable number of membrane bones; it is continued below into a *branchiostegal membrane* (Fig. 807, *br. m.*), which, except in Crossopterygii and the Sturgeons, is supported by bony rays. In Polypterus a pair of bony *jugular plates* (Fig. 823, B, *jug. pl.*) are placed at the lower end of the branchiostegal membrane, between the rami of the mandible: Amia has a single plate (Fig. 826, B, *jug. pl.*) in the same position. *Spiracles* are present only in Polypterus (Fig. 838) and some Sturgeons.

The commonest number of *median fins* is two dorsals, one caudal,

and one ventral, but this number may be increased or diminished (Figs. 828 and 830), or there may be a continuous median fin extending along the back and round the end of the tail to the vent. The dorsal fin is sometimes partly or wholly represented by a series of small *finlets* (Fig. 823). The tail-fin may be diphycercal, heterocercal, or homocercal, and is usually the chief organ of progression, but in the Sea-horse (Fig. 832) there is no caudal fin, and the tail is prehensile, being used in the position of rest to coil, in the vertical plane, round sea-weeds, &c.: when swimming it hangs downwards, having no lateral movement, and locomotion is effected by the vibration of the dorsal.

The *dermal rays* of the caudal fin are always jointed, as in the Trout, but in the Acanthopteri and Pharyngognathi more or fewer of the foremost rays of the dorsal, ventral, and pelvic fins are unjointed, forming *spines* (Figs. 829 and 830, *d. f.*), sometimes large and strong enough to recall the dermal defences of some Sharks and of Holocephali (Fig. 827, *d. f. r.* 1, *pct. f. r.* 1). In Polypterus (Fig. 823) each finlet is supported along its anterior edge by a strong spine, to which the soft rays are attached.

The anterior dorsal fin may attain an immense size, and is subject to some curious variations. In the Fishing-frog or Angler its foremost rays are elongated and bear lobes or lures by which small fishes are attracted as to the bait on a fishing-line.

In the Sucking-fish (*Echeneis*) the anterior dorsal is modified into an adhesive disc by means of which the fish attaches itself to the bodies of Sharks and Turtles.

The portion of the *paired fins* visible externally is usually very thin, and supported entirely by dermal rays. But in the Crossopterygii (Fig. 823) the rays form a fringe round a thick basal lobe, which is supported by endoskeletal structures (*vide infra*). This condition of things forms an approach to the structure met with in Elasmobranchs and Holocephali. The pectorals vary considerably in size, and in the Flying-fish (*Exocœtus*) form large, wing-like expansions, capable of sustaining the animal in its long flying leaps into the air. In the Butterfly-fish (*Gasterochisma*) the pelvic fins are similarly modified. In many Fishes the pelvics are reduced to filaments or scales, and in some cases a sucking-disc is developed in connection with them. The pectorals always retain their normal position, just behind the gill-cleft, but the pelvics always become more or less shifted forwards from their typical position beside the vent. The change in position is least in the three "ganoid" orders (Figs. 823–826) and in the Physostomi (Figs. 806 and 827), in which they are usually between the middle of the abdomen and the vent, and are said to be *abdominal* in position; but in a large proportion of the fishes in the remaining orders of Teleostei they come to be placed almost beneath the pectorals (Fig. 830, *pv. f.*), when their position is called

thoracic, or on the throat (Fig. 828), when they are said to be *jugular* in position.

A very remarkable deviation from the typical form occurs in the Flat-fishes (*Pleuronectidæ*), a family of Anacanthini. The body (Fig. 833) is very deep and strongly compressed: the fish habitually rests on the bottom, in some species on the right, in others on the left side, partly covering itself with sand, and occasionally swimming with a curious undulating movement. The under side is usually pure white, the upper side dark. The eyes (*r.e*, *l.e.*) are both on the upper or dark-coloured side, and the skull is distorted so as to adapt the orbits to this change of position. The abdominal cavity is very small, the vent placed far forward, and the dorsal

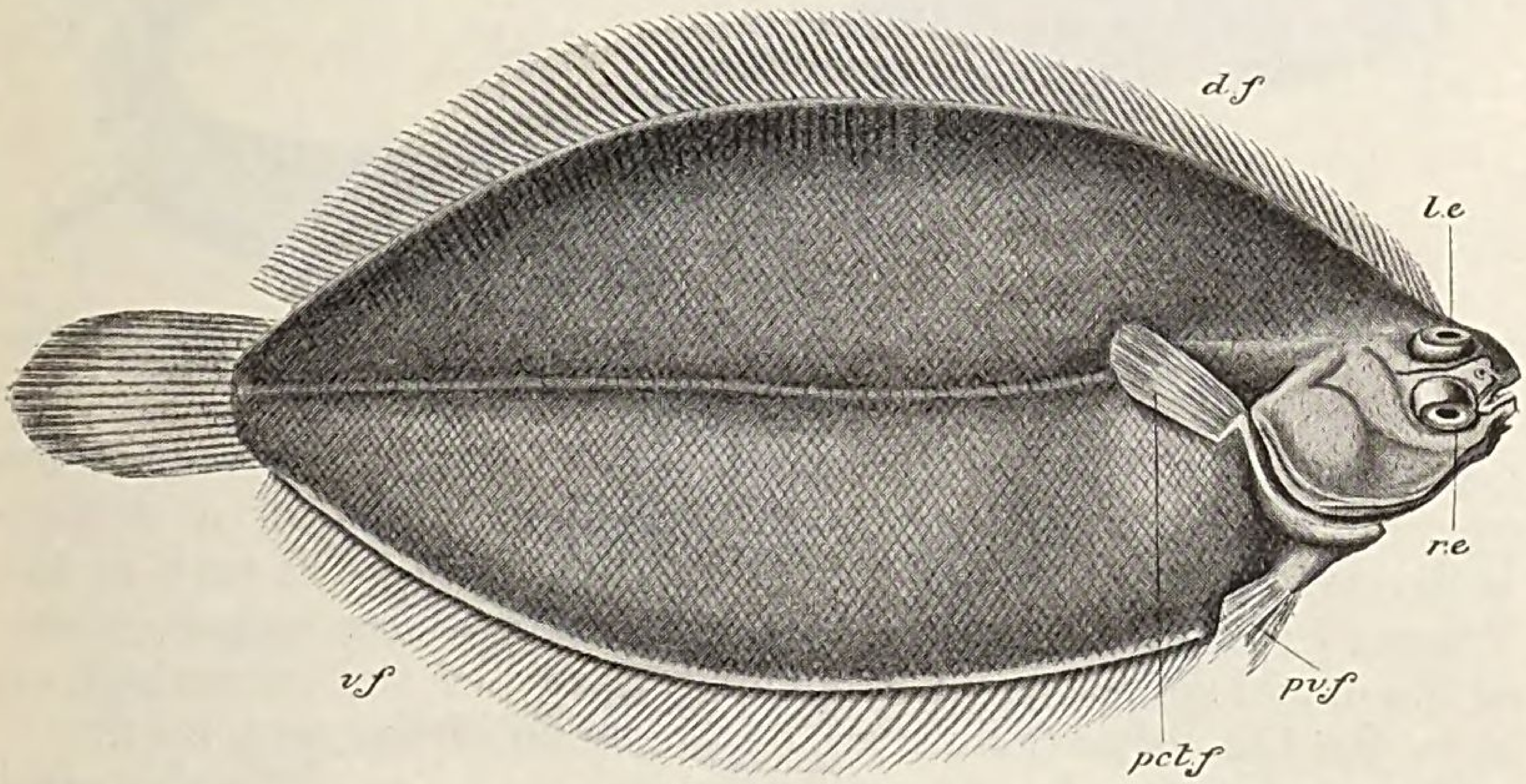


FIG. 833.—**Pleuronectes cynoglossus** (Craig-fluke), from the right side. *d. f.* dorsal fin; *l. e.* left eye; *pct. f.* pectoral fin; *pv. f.* pelvic fin; *r. e.* right eye; *v. f.* ventral fin. (After Cuvier.)

and ventral fins are continuous. Young Flat-fishes swim in the ordinary vertical position, but after a time they lie on one side and assume the adult peculiarities, the eye on the lower side gradually rotating until it reaches the upper surface.

Many Shore-fishes exhibit protective characters, the tints and markings of the skin being harmonised with those of the rocks, sea-weeds, &c., among which they live. The effect may be heightened by fringes and lobes of skin, resembling sea-weed, and often giving the fish a most grotesque appearance. The colours are often adaptable: Trout, for instance, alter their colour by the contraction or expansion of their pigment-cells, according to whether the streams in which they live have a muddy or a sandy bottom. In some Shore-fishes, such as those of the coral reefs the colours are of the most brilliant description; vivid reds, blues, and yellows, spots or stripes of gold or silver, are common, and, although the combination of tints may sometimes seem to our

eye rather crude and glaring, they appear to be distinctly protective, harmonising with the brilliant hues of the Coral Polypes and other members of the reef fauna. Pelagic fishes, such as the Mackerel and Herring, are usually steely-blue above, white beneath.

Many deep-sea Teleostei are phosphorescent: in some of these definite *luminous organs* (Fig. 834) are arranged in longitudinal

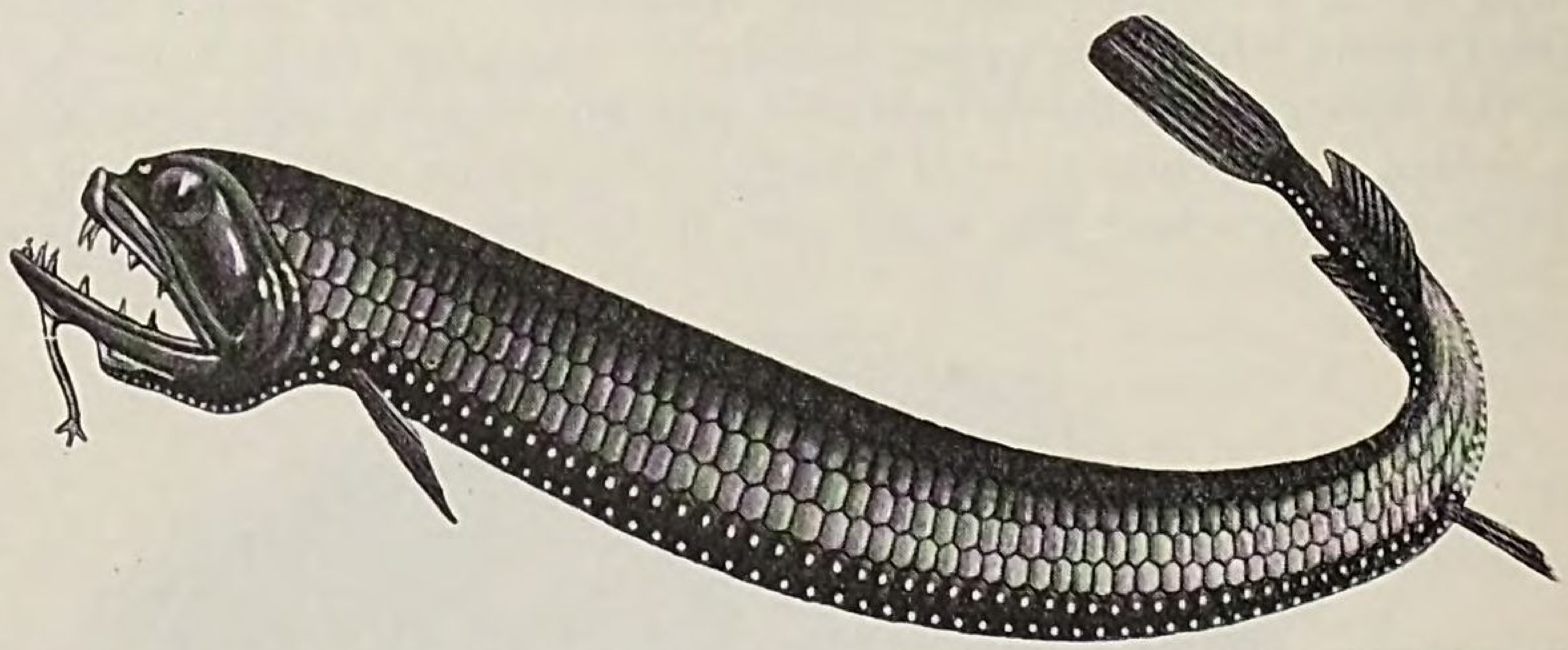


FIG. 834.—**Stomias boa.** The white dots are the luminous organs. (From Hickson., after Filhol.)

rows along the body, each provided with a lens, like that of the eye, the whole organ having thus the characters of a minute bull's-eye lantern. Some species of the same order, such as the Weaver (*Trachinus*), possess *poison-glands,* opening either on one of the dorsal spines, or on a spinous process of the operculum, or, as in the Cat-fishes (Siluridæ), on the spine of the pectoral fin.

Exoskeleton.—In many Teleostomi, such as Polyodon and the Eels, the skin is devoid of hard parts, but in most cases a dermal exoskeleton is present. In Amia and in the majority of Teleostei this takes the form, as in the Trout, of *scales,* rounded plates of bone imbedded in pouches of the derm and overlapping one another from behind forwards. When the free border of the scales presents an even curve, as in Amia and most Physostomi and Anacanthini, they are called *cycloid* scales (Fig. 808); when, as in most Acanthopteri, the free edge is produced into small spines (Fig. 835, A) they are distinguished as *ctenoid* scales. In exceptional cases the scales may be so large and strong as to form a rigid armour. In the Sturgeon (Fig. 824) there is a strong armour, formed of stout bony plates, or *scutes,*

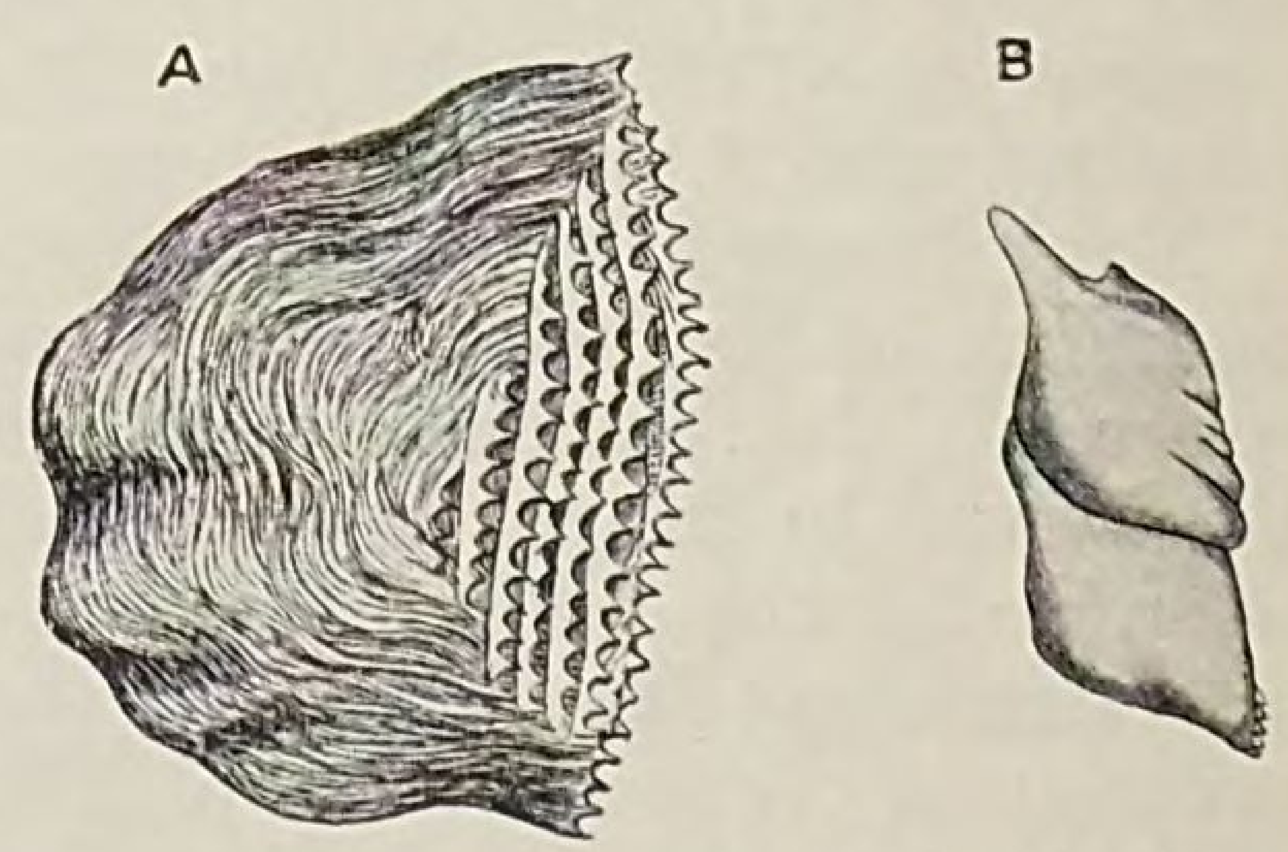


FIG. 835.—A, ctenoid scale; B, ganoid scales. (After Günther.)

produced into enamelled spines and articulating with one another by suture. Scutes are also found in many Siluroids (Fig. 827) and in Lophobranchii (Fig. 832) and some Plectognathi (Fig. 831), while in the Plectognathi the exoskeleton takes the form, as in the File-fishes, of minute spines like the shagreen of Sharks, or, as in many Globe-fishes, of long, outstanding, bony spines. Lastly, in Polypterus and Lepidosteus are found *rhomboid* or *ganoid* scales (Fig. 835, B), in the form of thick, close-set, rhomboidal plates formed of bone, covered externally by a layer of enamel or *ganoin*, and joined together by pegs and sockets. In many Ganoids the anterior fin-rays of both median and paired fins bear a row of spine-like scales called *fulcra* (Fig. 825, *fl.*).

Endoskeleton.—In the Sturgeon the *vertebral column* (Fig. 837 *WS.*) consists of a persistent notochord with cartilaginous arches

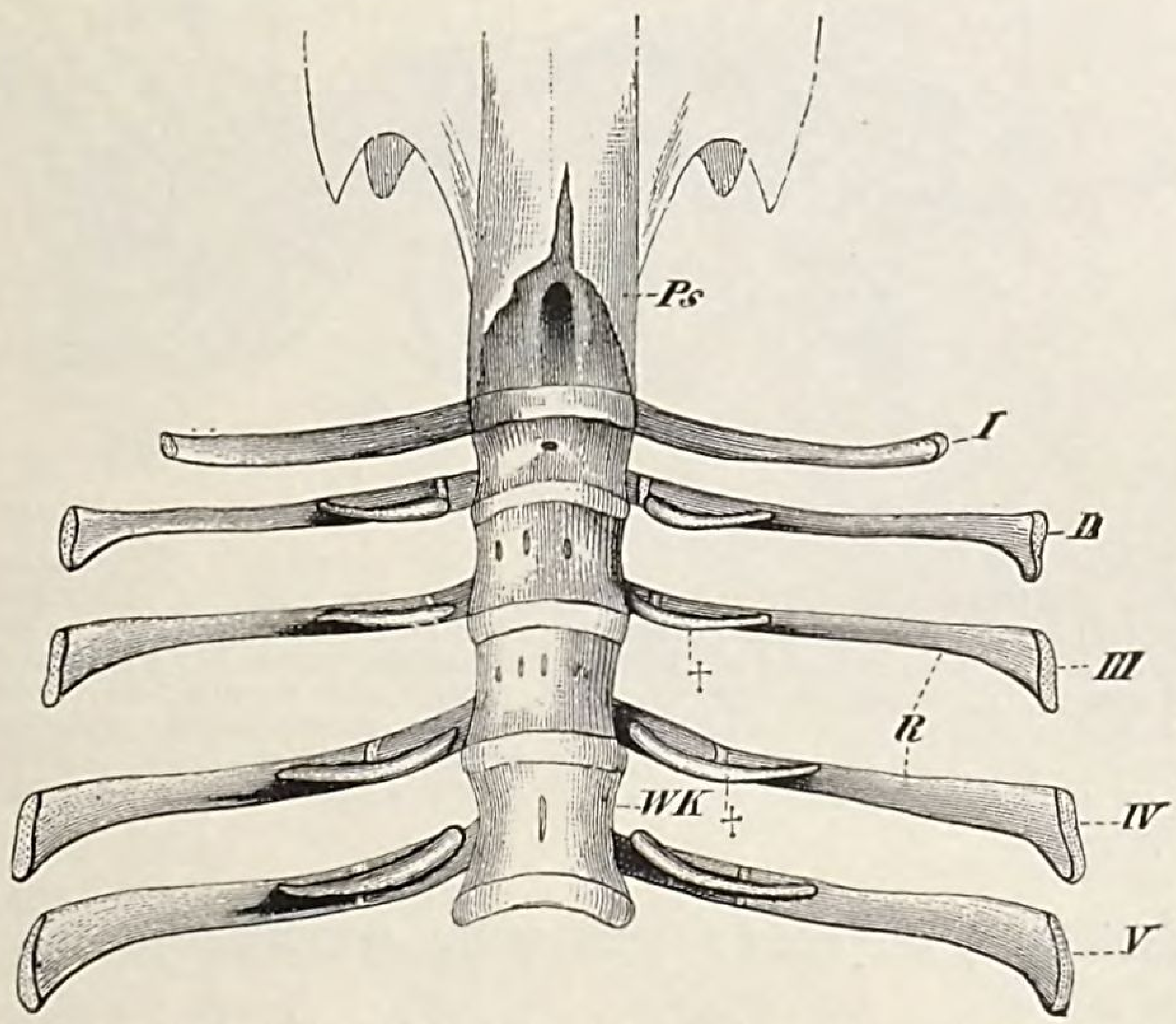


FIG. 836.—Anterior end of vertebral column of **Polypterus.** *PS.* parasphenoid; *R. I—V*, dorsal ribs; *WK*, centra; †, ventral ribs. (From Wiedersheim's *Comparative Anatomy*.)

and is fused anteriorly with the cranium. In the remaining orders bony vertebræ are present; the centra are biconcave, except in some Eels, in which the anterior face is flat or even convex, and in Lepidosteus, in which the anterior face is distinctly convex. Vertebræ of this form, *i.e.* having the centrum convex in front and concave behind, are called *opisthocœlous*. Ribs are usually present: in Polypterus each vertebra has two pairs, a dorsal pair (Fig. 836, *R*, *I—V*) of considerable length, running between the dorsal and ventral muscles, and a short ventral pair (†) between the muscles and the peritoneum: the former answer to the ribs of Elasmobranchs, the latter to the ribs of the remaining Teleostomi, which

are always placed immediately beneath the peritoneum. There may be one or more sets of intermuscular bones, attached either to the neural arch (*epineurals*), to the centrum (*epicentrals*), or to the ribs (*epipleurals*). The posterior end of the vertebral column is turned up in the Sturgeons, Lepidosteus, and Amia, resulting in a heterocercal tail-fin: in Amia, however, the fin-rays are so disposed that the fin appears almost symmetrical. Among Teleostei the tail-fin is rarely as obviously unsymmetrical as in the Trout: usually in the adult the development of the large, fan-shaped, posterior hæmal arches completely hides the upturned end of the notochord, and in some cases the spinal column ends simply in a somewhat compressed centrum around which the fin-rays

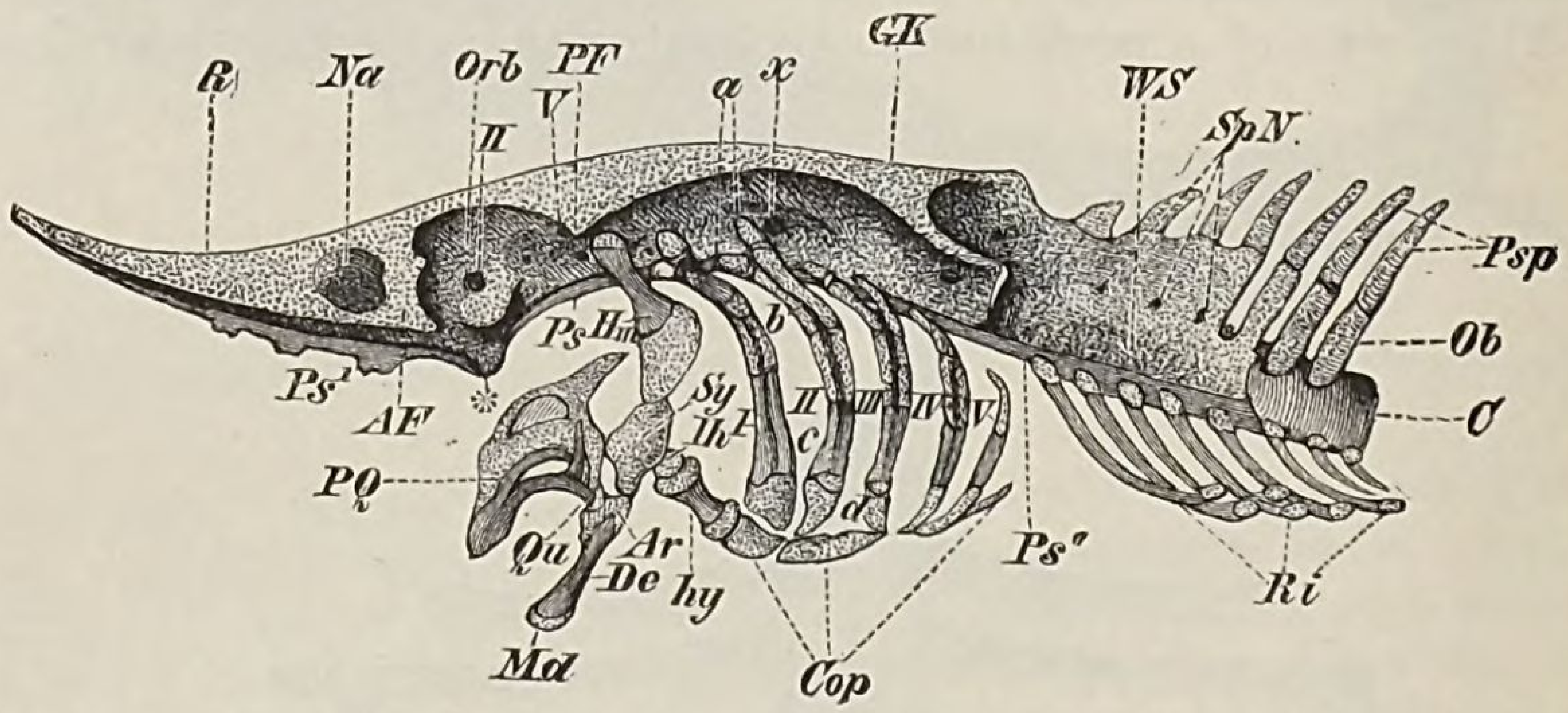


FIG. 837.—Skull of **Sturgeon**, with the membrane bones removed. *a*, pharyngo-branchial; *AF*, antorbital process; *AR.* articular; *b.* epibranchial; *c.* cerato-branchial; *C*, notochord; *Cop.* basi-branchials; *d*, hypobranchial; *De.* dentary; *GK*, auditory capsule; *HM.* hyomandibular; *hy.* hyoid cornu; *Ih.* inter-hyal; *Md.* mandible; *Na.* nasal capsule; *Gb*, neural arches; *PF*, post-orbital process; *PQ.* palato-quadrate; *Ps. Ps'. Ps''.* parasphenoid; *Psp.* neural spines; *Qu.* quadrate; *R.* rostrum; *Ri.* ribs; *Sp. N.* foramina for spinal nerves; *Sy.* symplectic; *WS*, vertebral column; *n*, vagus foramen; *I—V*, branchial arches. (From Wiedersheim's *Comparative Anatomy.*)

are symmetrically disposed; such truly symmetrical tail-fins are called *diphycercal*.

In the structure of the *skull* the Chondrostei make the nearest approach to Elasmobranchs. The cranium (Fig. 837) is an undivided mass of cartilage with a few isolated cartilage bones. The roofing membrane bones lie in the dermis, so as to be practically superficial, and behind pass insensibly into the scutes covering the trunk: the fact that these bones (parietals, frontals, &c.) are exoskeletal structures is here perfectly obvious. The same is the case in Polypterus (Fig. 838), in which, however, the cartilage bones are better developed. In Lepidosteus and Amia, and especially the latter, the skull resembles that of the Trout in all essential respects, the main differences consisting in the absence of certain bones, such as the supra-occipital, and in the presence of additional membrane bones. Among Teleostei it is only in the Physostomi that the membrane bones remain separable

from the chondrocranium in the adult; in the remaining orders, *e.g.* in the Cod, Haddock, or Perch, they become grafted on to the chondrocranium and so closely united with the cartilage bones that they can be removed only by pulling the whole skull to pieces; most of the original cartilage frequently disappears in the adult, and the cranium thus becomes a firm bony mass in which no distinction between cartilage and membrane bones is discernible.

The varying size of the gape, which is so noticeable a feature in the Teleostomi depends upon the inclination of the suspensorium; in wide-mouthed Fishes (Fig. 828) the axis of the hyomandibular and suspensorium is nearly vertical or even inclined backwards: in small-mouthed forms (Fig. 831) it is strongly inclined forwards and the length of the jaws is proportionately reduced. In the branchial arches the pharyngo-branchials of each side are very commonly fused, and constitute what are called the *superior pharyngeal bones:* the reduced fifth branchial bars, or *inferior pharyngeal bones,* bite against them. The Pharyngognathi are distinguished by having the inferior pharyngeal bones united into a single bony mass of characteristic form (Fig. 830, B). The gill-rakers are often very highly developed, and may form a mesh capable of retaining even microscopic organisms.

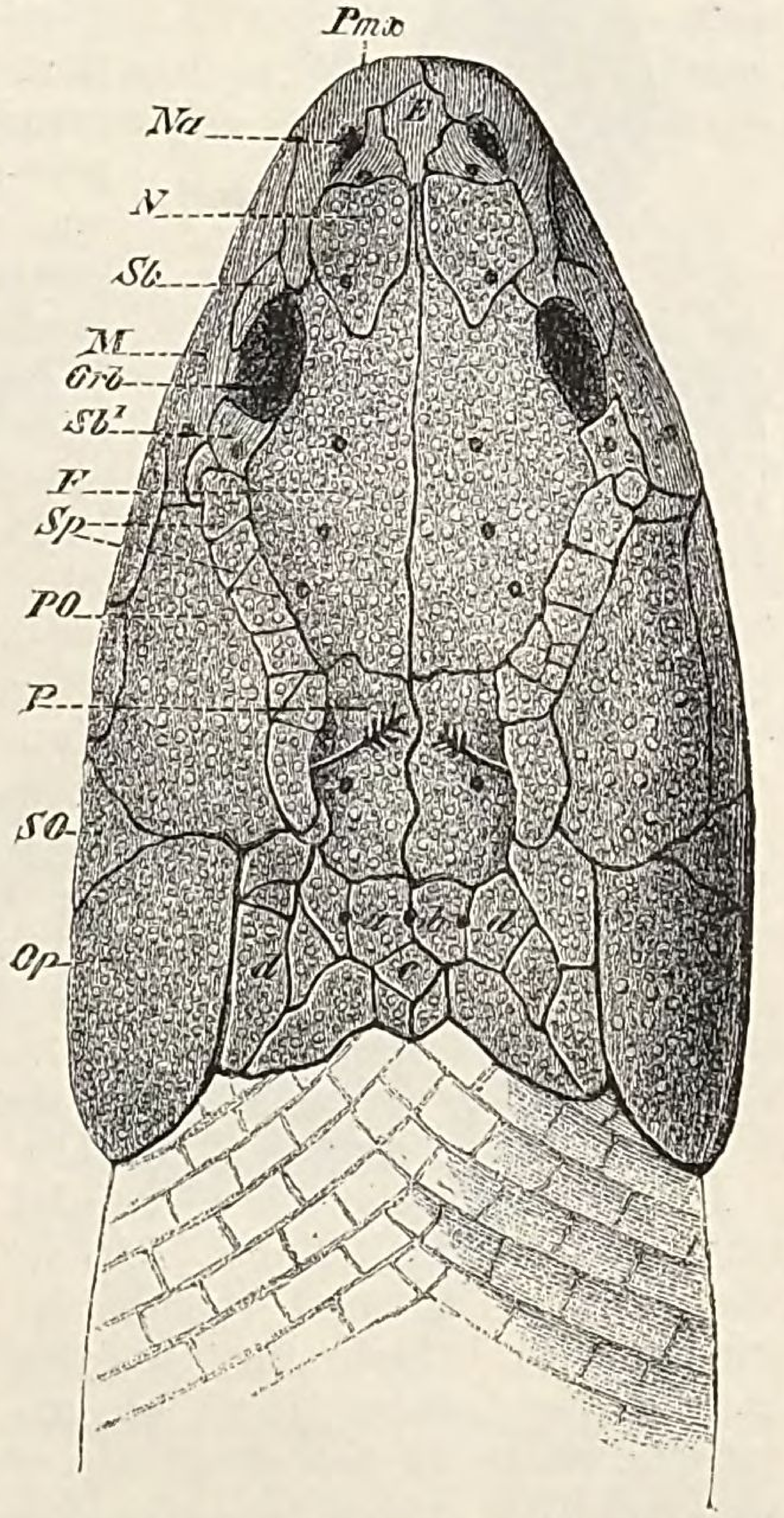


FIG. 838.—Skull of **Polypterus,** from above. *F.* frontal; *M.* maxilla; *NA.* nasal; *Na.* nostril; *Op.* opercular; *Orb.* orbit *P.* parietal. The remaining letters point to less important membrane bones. The arrow is passed into the spiracle. (From Wiedersheim's *Comparative Anatomy.*)

In the *shoulder-girdle,* as in the skull, the Chondrostei approach the Elasmobranchs. There is a primary shoulder-girdle consisting of large paired cartilages, not united in the middle ventral line, and unossified: each is covered externally by a large scute-

like membrane-bone, the *clavicle*. In the remaining Ganoids and in Teleostei, the primary shoulder-girdle is reduced in size and is usually ossified by two bones, a dorsal *scapula* and a ventral *coracoid*: sometimes, as in the Trout, there may be an additional ossification, the meso-coracoid. Additional membrane bones—supra-clavicle, post-clavicle, &c.—are added, and one of them, the post-temporal, serves to articulate the shoulder-girdle with the skull (Fig. 815).

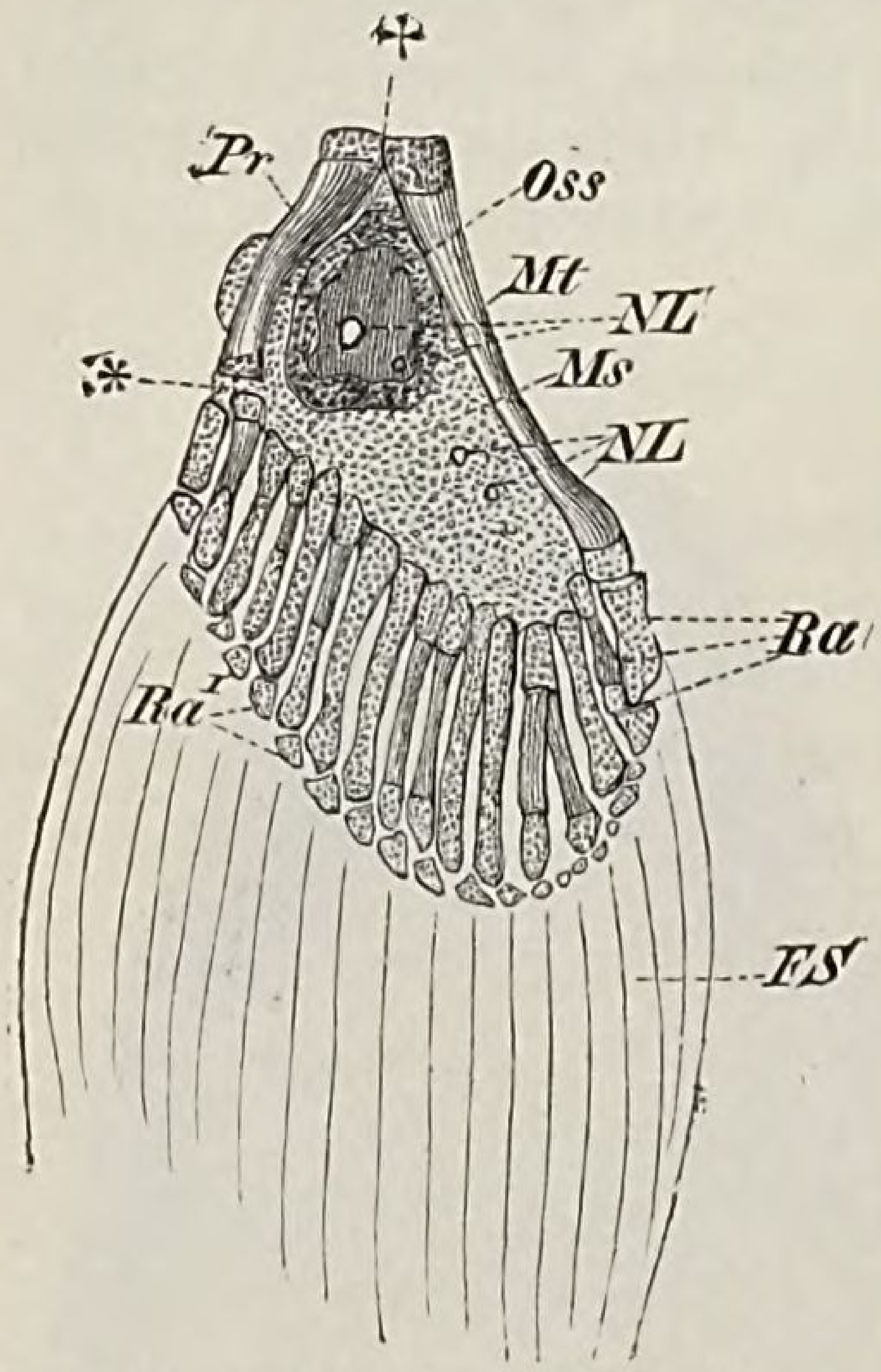


FIG. 839.—Pectoral fin of **Polypterus**. *FS.* dermal rays; *MS.* mesopterygium; *MT.* metapterygium; *NL,* nerve-foramina; *Oss.* ossification in mesopterygium; *Pr.* propterygium; *Ra.* first radials; *Ra'.* second radials. (From Wiedersheim's *Comparative Anatomy.*)

In the skeleton of the *pectoral fin* it is the Crossopterygii which approach most nearly to Elasmobranchs. In Polypterus (Fig. 839) the basal lobe of the fin is supported by a rod-like ossified propterygium (*Pr*), a broad cartilaginous mesopterygium (*MS*), and an ossified metapterygium (*MT*); to these, two rows of elongated radials (*Ra*, Ra^1) are articulated fan-wise, and these in their turn give attachment to the fin-rays (*FS*). In all the remaining orders the basalia (pro-, meso-, and metapterygium) are absent, and the endoskeleton of the fin consists only of a single or double row of radials (Fig. 815).

In Polypterus there is a vestigial *pelvic girdle* (Fig. 839 *bis*, *BP*) in the form of a small rhomboidal cartilage to which the anterior ends of the basalia (Bas^1) are attached: thus in the structure of the posterior extremities also, the Crossopterygii are the most primitive of the Teleostomi. In all the remaining orders the pelvic girdle is atrophied. The *pelvic fin* is supported by a single bone of variable form (Fig. 816, BSTG) and representing a *basale*, *i.e.* a structure arising from the fusion of proximal pterygiophores. Between its posterior end and the dermal rays irregular nodules, representing radials, may be interposed.

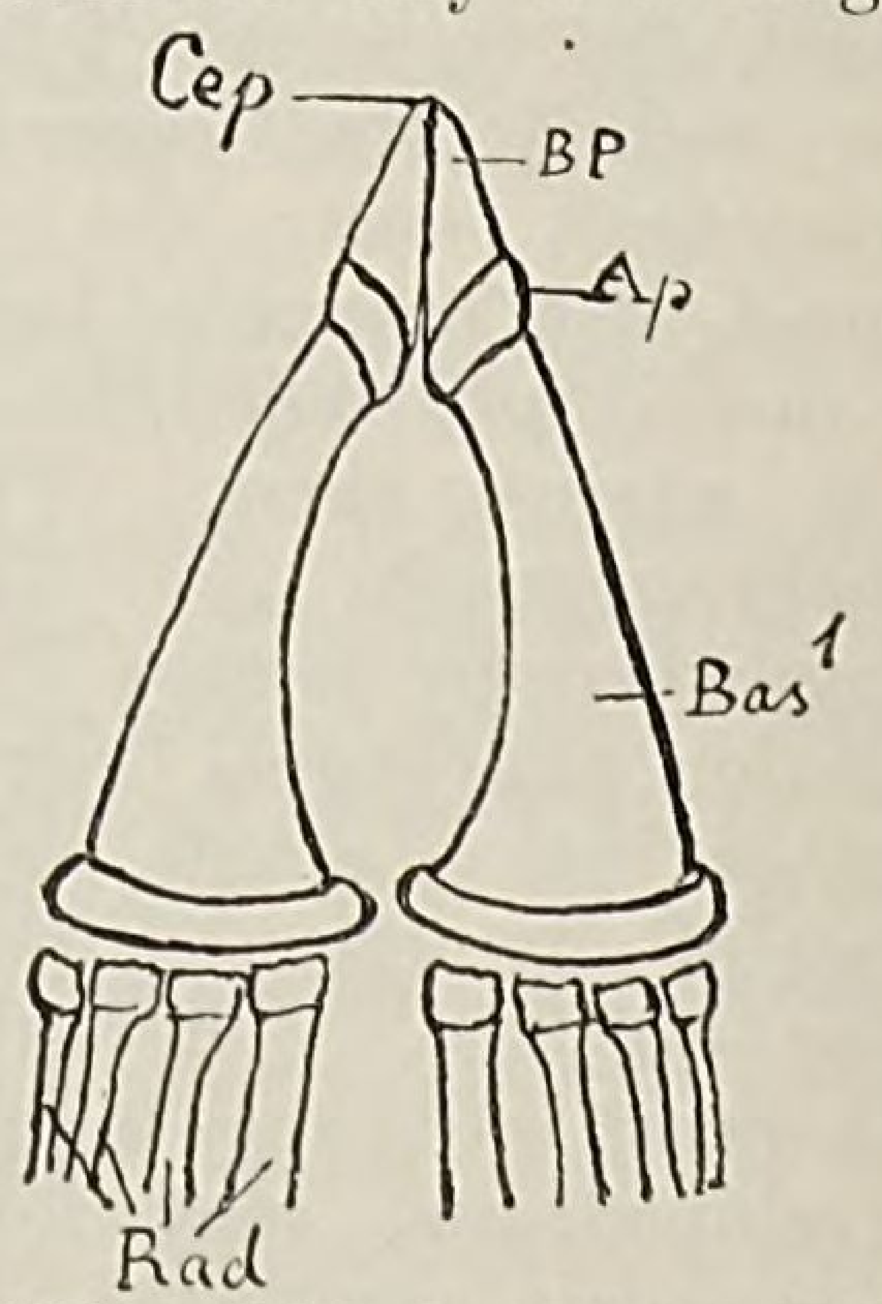


FIG. 839 *bis*.—Pelvic fin of young **Polypterus**. *Ap.* part of basale; Bas^1. basale; *BP.* pelvic cartilages (fused in adult); *Cep.* epipubis; *Rad.* radials. (From Wiedersheim.)

The distinction between hard or unjointed fin-rays, or spines, and soft or jointed fin-rays has already been referred to. The first ray of the dorsal and pectoral fins sometimes, *e.g.* in Siluroids (Fig. 827), has the form of a very strong spine articulated by a bolt-and-shackle joint, *i.e.* by the interlocking of two rings. In some cases the first dorsal spine springs from the skull.

The texture of the bones is subject to wide variation: in some Acanthopteri they are very thick and strong, in some places almost like ivory, while in the Lump-fish (*Cyclopterus*), the huge Sunfish (*Orthagoriscus*), and in many deep-sea forms, such as the Ribbon-fishes (*Regalecus* and *Trachypterus*), the amount of mineral matter is so small that the bones are easily cut with a knife and weigh astonishingly little when dry.

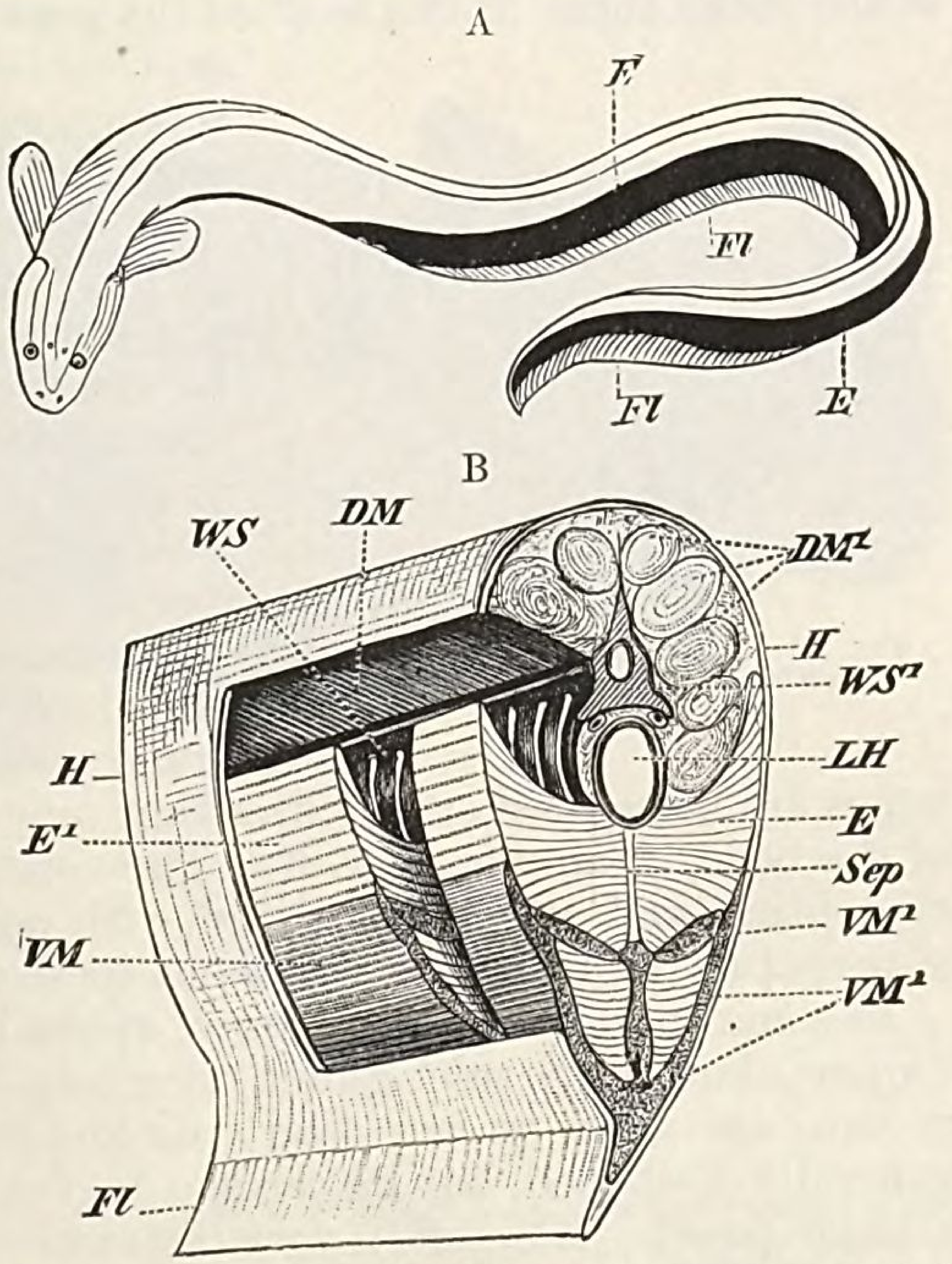


FIG. 840.—**Gymnotus electricus,** showing the extent of the electric organ (*E*). *Fl*, ventral fin. B, small portion of tail, in section. *DM. DM.'* dorsal muscles; *E. E'.* electric organ; *Fl*, ventral fin; *H*, skin; *LH*, caudal canal; *Sep.* fibrous septum; *VM. VM'.* ventral muscles; *WS, WS'*, vertebral column, with spinal nerves. (From Wiedersheim's *Comparative Anatomy*.)

Electric organs. Two genera of Teleostomi possess electric organs, the Electric Cat-fish (*Malapterurus*), one of the Siluridæ, found in the fresh waters of tropical Africa, and the Electric Eel (*Gymnotus*), a Physostome occurring in Brazil and the Guyanas. In Malapterurus the electric organ extends over the whole body, beneath the skin; in Gymnotus (Fig. 840) there are two pairs of batteries in the ventral half of the greatly elongated tail.

Digestive organs.—Some Teleostomi are toothless; but in most instances *teeth* are present, and may be developed on the premaxilla, maxilla, palatine, pterygoid, vomer, dentary, basihyal, and superior and inferior pharyngeal bones. It is characteristic of most Teleostei, with the exception of Physostomi, that the maxilla is edentulous (Fig. 829) and does not enter into the gape.

In a large majority of species the teeth are small, conical, and recurved, suitable for preventing the struggling prey from slipping out of the mouth, but quite unfitted for either tearing or crushing. In some Fishes, such as the Pike, the teeth are hinged backwards so as to offer no resistance to the passage of the prey towards the gullet, but effectually barring any movement in the other direction. In many deep-sea Fishes (Fig. 834) the teeth are of immense size and constitute a very formidable armature to the jaws. Many instances occur in which there is a marked differentiation of the teeth, those in the front of the jaws (Fig. 841) being pointed or chisel-edged, and adapted for seizing, while the back teeth have spherical surfaces adapted for crushing. In the Wrasses (Fig. 830, *B*) strong crushing teeth are developed on the pharyngeal bones. In the Globe-fishes the teeth are apparently reduced to one or two in each jaw, but each "tooth" in this case really consists of numerous calcified plates fused together. The teeth may be either simply imbedded in the mucous membrane so as to be detached when the bones are macerated or boiled, or they may be implanted in sockets of the bone, or ankylosed to it. They are formed of some variety of dentine, and are often capped with enamel. Their succession is perpetual, *i.e.* injured or worn-out teeth are replaced at all ages.

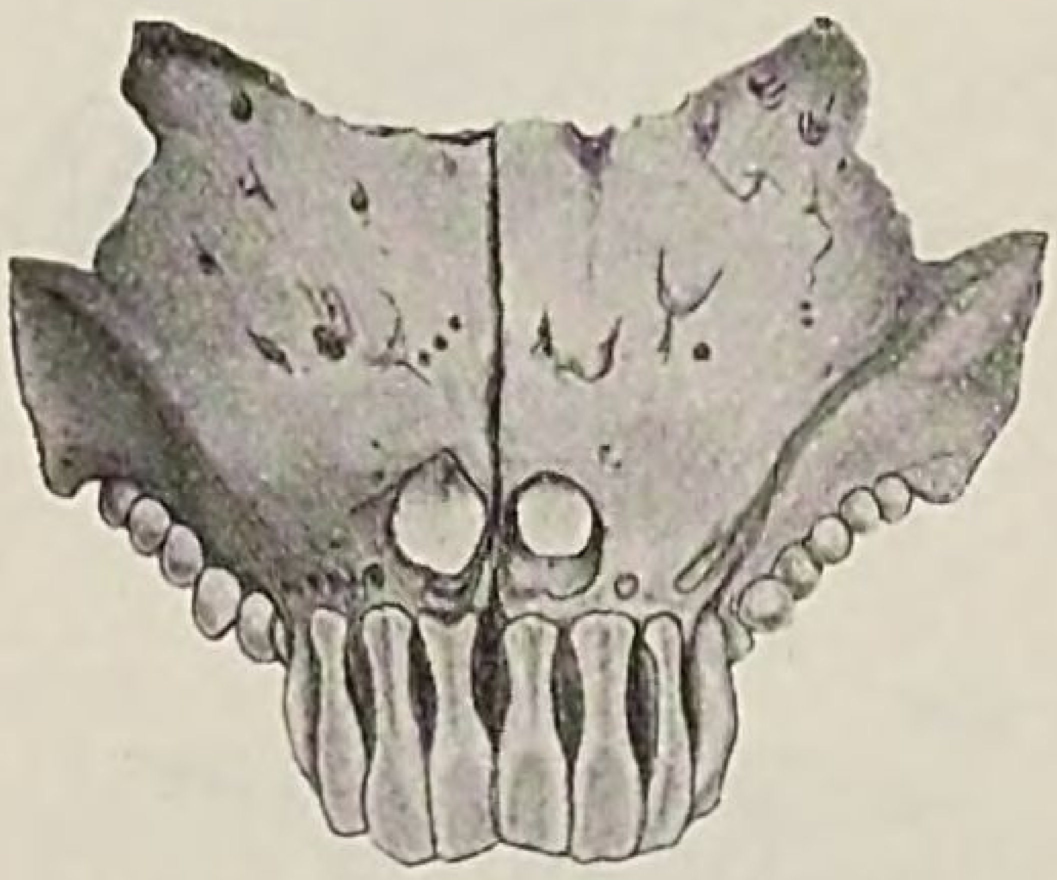


FIG. 841.—Premaxillæ of **Sargus**, showing teeth. (After Owen.)

In some species the *enteric canal* shows little differentiation into regions, but, as a rule, gullet, stomach, duodenum, ileum, and rectum are more or less clearly distinguishable. The *stomach* is generally V-shaped, but its cardiac region may be prolonged into a blind pouch; it is often very distensible, allowing some of the deep-sea Teleostei to swallow Fishes as large as themselves. In the Globe-fishes the animal can inflate the gullet with air, when it floats upside down on the surface of the water. The Ganoids have a *spiral valve* in the intestine, which is very well developed in Polypterus and the Sturgeon, vestigial in Lepidosteus (Fig. 843, *sp. v.*) and Amia: it is absent in all Teleostei, except possibly in *Chirocentrus*, one of the Physostomi. The liver is usually large; a pancreas may be present as a compact gland, as in Elasmobranchs, or may be widely diffused between the layers of the mesentery. *Pyloric cæca* are commonly present, and vary in number from a single one to two hundred. The anus is always distinct from, and in front of, the urino-genital aperture.

Respiratory organs.—The gills are usually comb-like, as in the Trout, the branchial filaments being free, owing to the atrophy

of the interbranchial septa. In the Sturgeon, however, the septa are fairly well developed, reaching half-way up the filaments, so that the latter are free only in their distal portions; this arrangement is obviously intermediate between the Elasmobranch and Teleostean conditions. The most striking deviation from the normal structure occurs in Lophobranchii, in which the gill-filaments are replaced by curious tufted processes (Fig. 832, B *g.*). As a rule gills (holobranchs) are developed on the first four branchial arches, but the fourth is frequently reduced to a hemibranch, and further reduction takes place in some cases. The

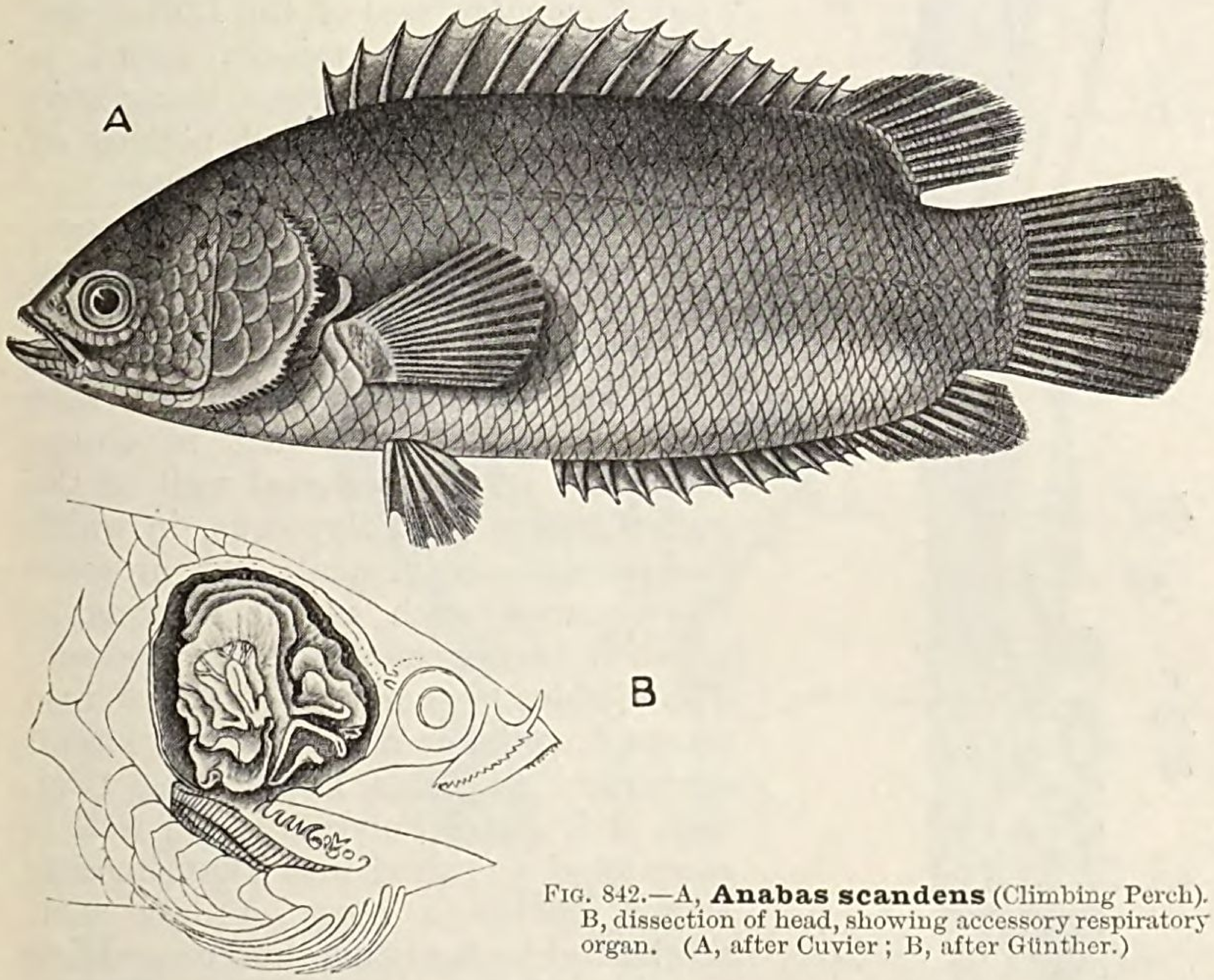


FIG. 842.—A, **Anabas scandens** (Climbing Perch). B, dissection of head, showing accessory respiratory organ. (A, after Cuvier; B, after Günther.)

pseudobranch or vestigial hyoidean gill may either retain the characteristic comb-like structure, as in the Trout, or may be reduced, as in the Cod, to a gland-like organ formed of a plexus of blood vessels and called a *vaso-ganglion* or *rete mirabile*.

In addition to the gills some Teleostei possess accessory organs of respiration. In *Amphipnous*, an Indian Physostome, the gills are poorly developed and are functionally replaced by a vascular sac occurring on each side of the body and opening in front into the first (hyo-branchial) gill-cleft. Such sacs are physiologically, though not morphologically, lungs. In the Climbing Perch (*Anabas*) of the Oriental Region (Fig. 842) the superior pharyngeal bones are developed into folded plates (B) covered with vascular

mucous membrane and capable of retaining water for a considerable period; the Fish is able to traverse the land, and is even said to climb trees, holding on alternately by the spines of its pre-operculum and of its ventral fins. It has become so thoroughly a land animal that it is drowned if immersed in water. In the little armoured Siluroid *Callichthys*, anal respiration takes place, air being drawn into and expelled from the rectum. And, lastly, in the curious little goggle-eyed *Periophthalmus* of the Indian and Pacific Oceans the tail-fin seems to serve as a respiratory organ, being kept in the water while the Fish perches on a rock.

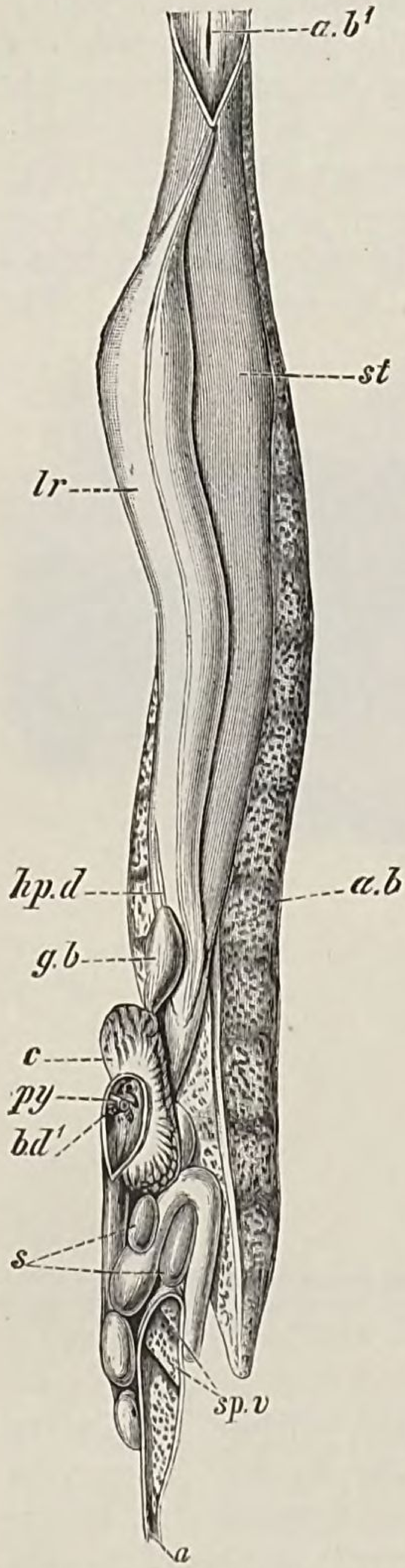


FIG. 843.—Digestive organs and air-bladder of **Lepidosteus.** *a.* anus; *a. b.* air-bladder; *a.b'.* its aperture in the pharynx; *b. d.* aperture of bile-duct; *c.* pyloric cœca; *g. b.* gall-bladder; *hp. d.* hepatic duct; *lr.* liver; *py.* pyloric valve; *s.* spleen; *sp. v.* spiral valve; *st.* stomach. (From Wiedersheim's *Comparative Anatomy*.)

The **air-bladder** retains its connection with the gullet in Ganoids and Physostomes; in the other Teleostei the pneumatic duct atrophies in the adult, and the bladder becomes a shut sac. The pneumatic duct is always connected with the dorsal wall of the gullet except in Polypterus, in which the aperture is ventral, and in some Physostomes, such as the Herring, in which it is connected with the stomach. The bladder is sometimes divided into compartments or produced into lateral offshoots: in Amia, Lepidosteus (Fig. 843, *a. b.*), and Polypterus its wall is sacculated or raised into anastomosing ridges, enclosing more or less well-marked chambers and thus resembling a lung. In Polypterus its lung-like character is enhanced by its division into two compartments by a longitudinal partition, as well as by the ventral position of the opening of the pneumatic duct.

The air-bladder seems able to act as a sort of accessory respiratory organ; it has been found that in a Perch, asphyxiated in stagnant water, the oxygen in the bladder, which normally amounts to 20 or 25 per cent., is entirely absorbed and replaced by nitrogen and carbonic acid. Its normal

function, however, is hydrostatic, *i.e.* it serves to keep the Fish of the same specific gravity as the water. Variations in pressure as the Fish ascends or descends are regulated by absorption or secretion of gas, often by means of vaso-ganglia or *red glands* (Fig. 844, *vs. gn.*) in the walls. These are elevations of the wall of the bladder, abundantly supplied with blood, and having tubular glands which open into the cavity of the bladder and secrete a fluid of unknown function. In Fishes with a pneumatic duct the red glands are

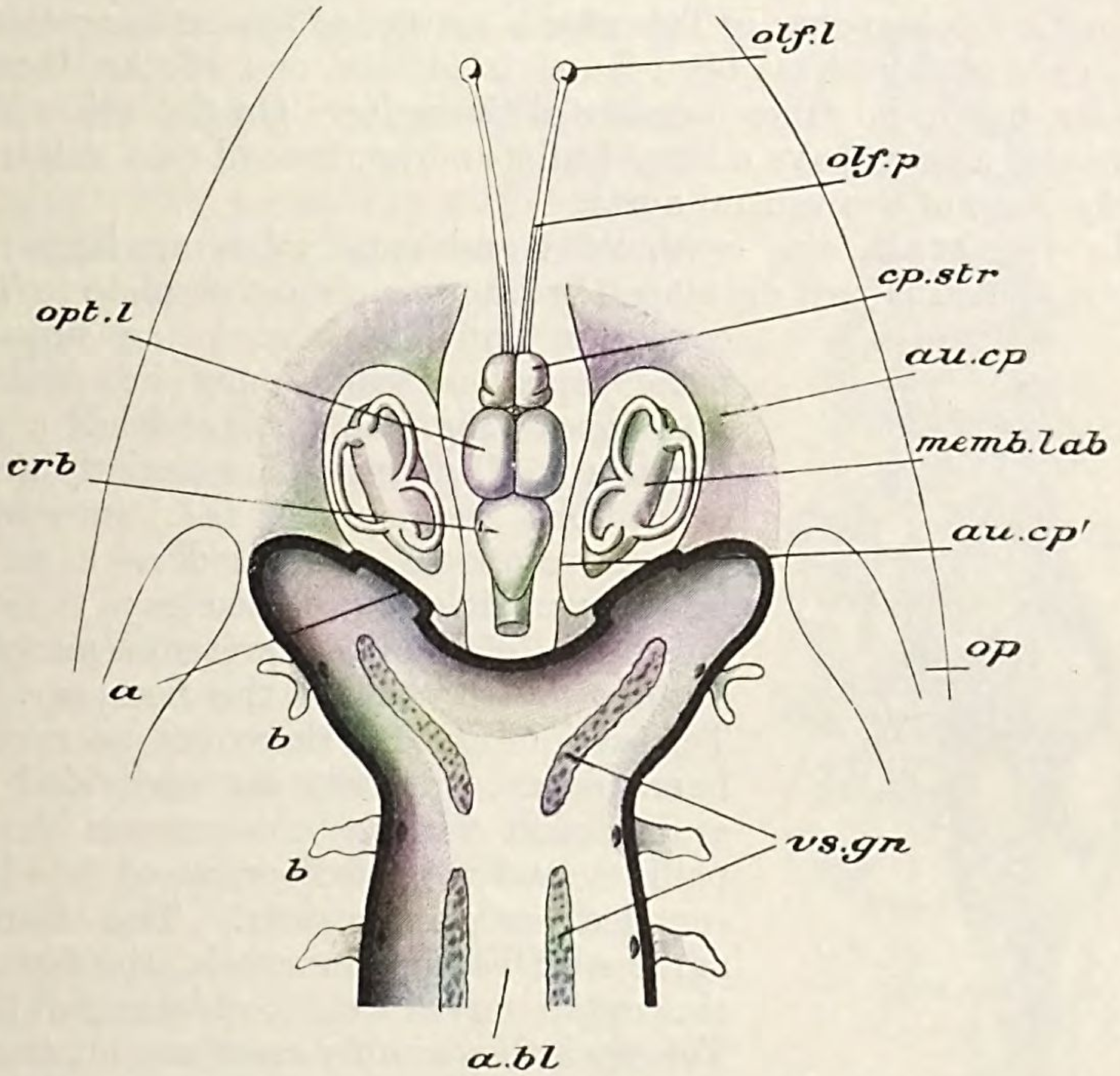


FIG. 844.—Horizontal section of posterior portion of head and anterior end of air-bladder in **Pseudophycis bachus**, one of the Gadidæ or Cods (semi-diagrammatic). *a*, thickened portion of air-bladder fitting into fenestra in posterior wall of auditory capsule; *a. bl.* air-bladder; *au. cp.* outer wall of auditory capsule; *au. cp.′* inner (membranous) wall; *b*, hollow offshoots of air-bladder; *cp. str.* corpora striata; *crb.* cerebellum; *memb. lab.* membranous labyrinth; *olf. l.* olfactory lobes; *olf. p.* olfactory peduncles; *op.* operculum; *opt. l.* optic lobes; *vs. gn.* vaso-ganglia.

absent, but in Eels their place is taken by *red bodies* of similar appearance but with non-glandular epithelium. In some forms with closed air-bladder the anterior end of the organ is forked, and each branch (*a*) fits closely against a membranous space in the posterior wall of the auditory capsule, while laterally it extends outwards in the region of the shoulder-girdle, and comes to lie immediately beneath the skin; in this way varying pressures on the surface of the body are transmitted through the air in the bladder to the auditory

organ. In the Carps and Siluroids a chain of bones connects the air-bladder with the auditory organ, forming the *Weberian apparatus*, the function of which, as of the simpler arrangement described above, is probably "to bring directly to the consciousness of the Fish the varying tensions of the gaseous contents of the air-bladder, due to the incidence of varying hydrostatic pressures."

The structure of the **heart** forms one of the most striking differences between the three Ganoid orders and the Teleostei. In Ganoids there is a muscular conus arteriosus with rows of valves, as in Elasmobranchs; in Teleostei a vestige of the conus containing two rows of valves has been found in *Albula*, one of the Herring family, but in no other member of the order. On the other hand, Teleostei always have a large bulbus aortæ, formed as a dilatation of the base of the ventral aorta.

In the **brain** the cerebellum and optic lobes are large; the diencephalon is well developed in Ganoids, almost obsolete in Teleostei. In Ganoids there is an unpaired prosencephalon, which may be produced into lobes (Fig. 845, *prs.*) and has a non-nervous roof, giving off anteriorly a pair of cerebral hemispheres (*c.h.*) into which the prosocœle is continued as a pair of lateral ventricles or paracœles; thus the fore-brain of Ganoids presents many resemblances to that of the Lamprey. In Teleostei (Fig. 818) there are no cerebral hemispheres, but only an undivided prosencephalon with a non-nervous roof or pallium, and with its floor raised into large rounded corpora striata. The Ganoids agree with Elasmobranchs in the fact that the optic nerves form a chiasma, while in Teleostei they simply cross one another or decussate. Here also, however, the distinction is not quite absolute, since in the Herring and some other Physostomes one nerve passes through a slit in the other. In some cases the olfactory lobes spring directly from the prosencephalon, as in the Trout; in others they are borne on long *olfactory peduncles* (Fig. 844, *olf. p.*), as in the Cod. In some Plectognaths the spinal cord undergoes a remarkable shortening: in a Sun-fish $2\frac{1}{2}$ metres in length and weighing a ton and a half, the cord is only 15 millimetres long, being actually shorter than the brain.

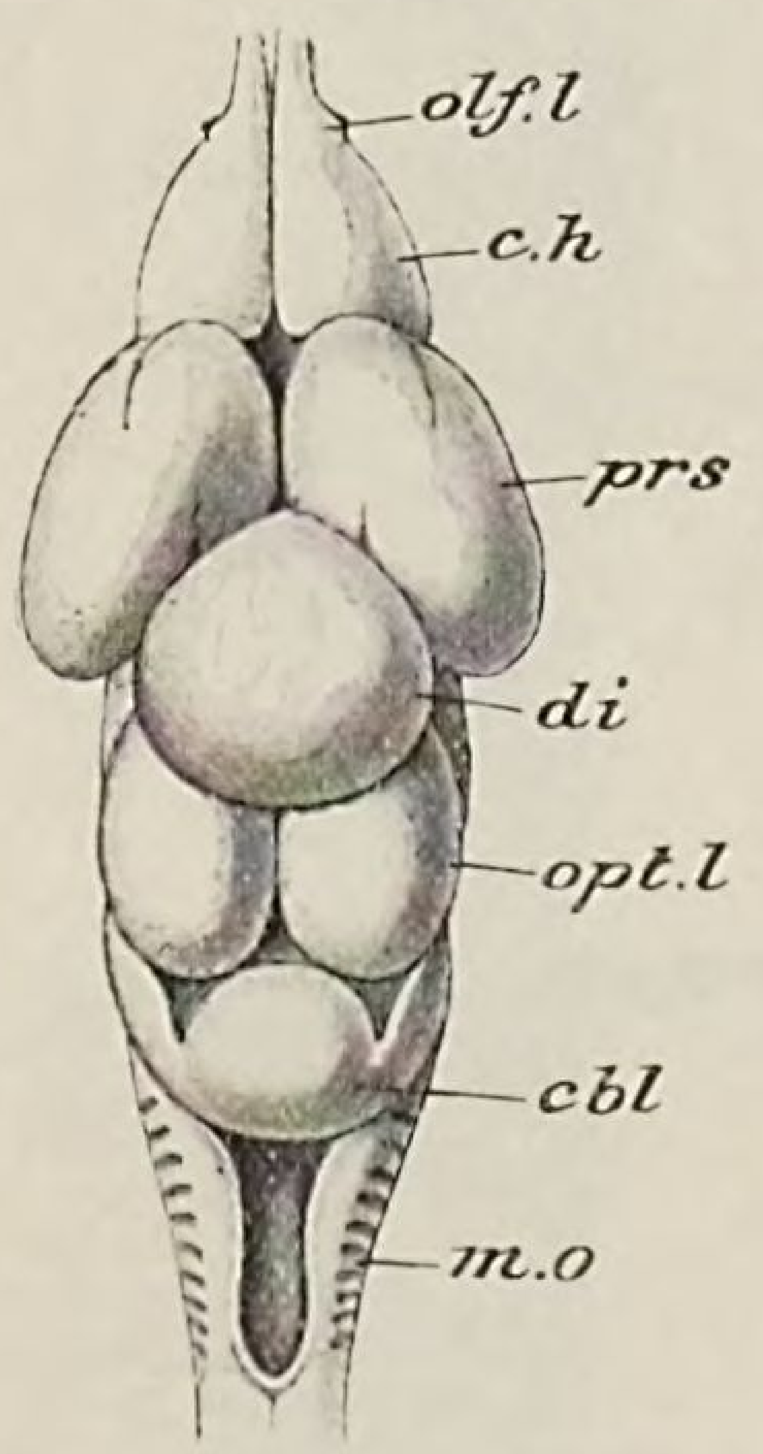


FIG. 845.—Brain of **Lepidosteus,** dorsal view. *cbl.* cerebellum; *c. h.* cerebral hemispheres; *di.* diencephalon; *m. o.* medulla oblongata; *olf. l.* olfactory lobes; *opt. l.* optic lobes; *prs.* lobes of prosencephalon. (After Balfour and Parker.)

Urino-genital Organs.—The *kidney* (Fig. 817, *kd.*) is formed from the mesonephros of the embryo and usually attains a great

size; the pronephros usually atrophies. The *ureter* (*ur.*) is the undivided segmental duct: it unites with its fellow of the opposite side before opening either directly on to the exterior or into a urino-genital sinus. A *urinary bladder* is formed as a single or double dilatation of the ureter. The right and left kidneys undergo more or less fusion, and their anterior ends are usually converted into adenoid or lymphatic tissue (*kd'.*), so that, while resembling the rest of the organ in external appearance, they do not discharge a renal function.

The *male organs* of Lepidosteus may be taken as an example of those of Ganoids. The testis (Fig. 846, *ts.*) is a paired lobulated organ, the secretion of which is carried by a large number of vasa efferentia (*v. ef.*) into a longitudinal canal (*l. c.*) lying alongside the ureter (*ur.*). From this canal tubes are given off which communicate with the urinary tubules of the kidney, so that the seminal fluid has to traverse these tubules in order to reach the urinary bladder (*bl.*) and make its escape by the common urinogenital aperture (*u.g. ap*). In Teleostei there are no vasa efferentia, but the posterior end of the testis is directly continued into a duct (Fig. 817, *v. d.*) which unites with its fellow of the opposite side and opens either into a urino-genital sinus, as in the Trout, or, as in the Cod, directly on to the exterior, between the anus and the urinary aperture. In the Eels the seminal fluid escapes into the cœlome and is discharged by genital pores.

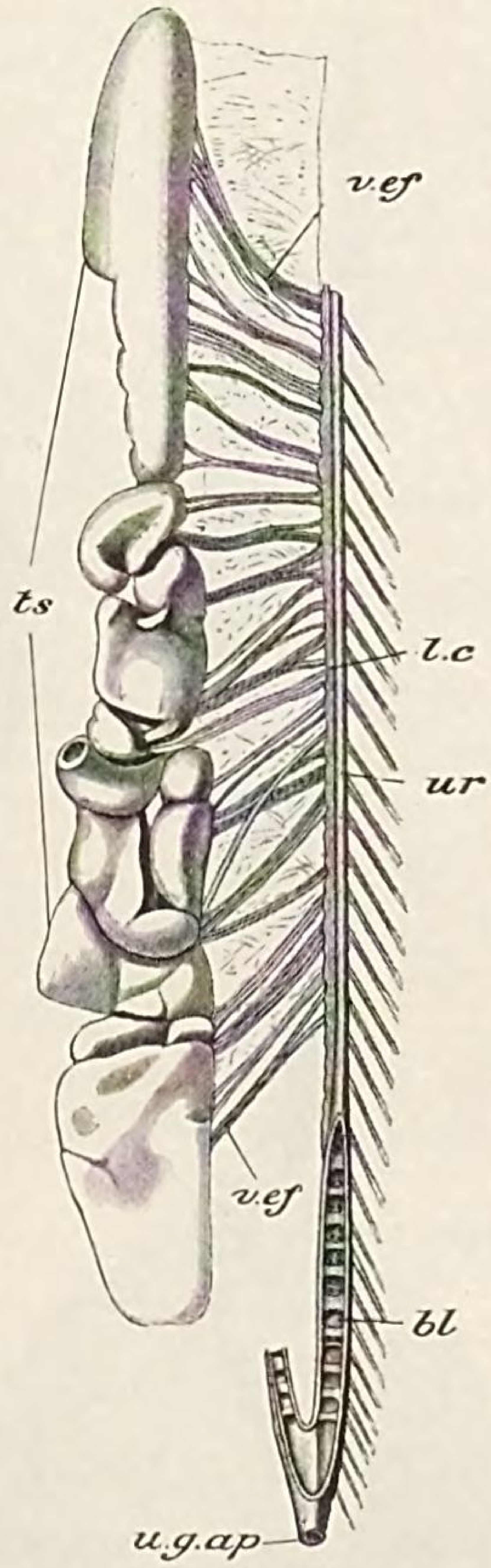


FIG. 846.—Male organs of **Lepidosteus.** *bl.* bladder; *l. c.* longitudinal canal; *ts.* testis; *u.g. ap.* urino-genital aperture; *ur.* ureter; *v. ef.* vasa efferentia. (After Balfour and Parker.)

In most Ganoids the *oviducts* (Fig. 847, B, *ovd.*) have funnel-like anterior ends (*ovd.''*) opening into the cœlome, while posteriorly (*ovd.'*) they discharge into the dilated ureters (*bl.*). A similar arrangement occurs in the Smelt, one of the Physostomi, in which the eggs are discharged from the outer or lateral face of the ovary into the open end of the oviduct. But in most Teleostei and in Lepidosteus (Fig. 847, A) the ovary (*ovy.*) is a hollow sac continued posteriorly into the oviduct (*ovd.*): the eggs are set free into its cavity from the folds into which its inner surface is produced, and

so pass directly into the oviduct without previously entering the cœlome. An ovary of this kind reminds us of the state of things in Arthropods, in which also the ovary is a hollow organ discharging its products into its internal cavity, whence they pass directly into the continuous oviduct. It was pointed out that the lumen of the ovary in this case was to be looked upon as a shut-off portion of the cœlome: this is certainly the case in Lepidosteus and Teleostei. In the embryo a longitudinal fold grows from the ventral edge of the then solid ovary, and turns upwards along the lateral face of the organ: it is met by a descending fold of peritoneum from the dorsal wall of the abdomen, and by the union of the two folds a cavity is enclosed, which is the lumen of the ovary. The oviduct is developed as a backward continuation of these folds of peritoneum, and appears to be quite unconnected with the embryonic nephridial system, and therefore not to be homologous with the oviducts of Elasmobranchs and Holocephali, which, as we have seen, are Müllerian ducts. In the Salmonidæ and the Eels oviducts are absent, and the ova are discharged by genital pores, which are probably to be looked upon as degenerate oviducts. True abdominal pores are present in Ganoids and in some Physostomi. Most Teleostomi are diœcious, but *Serranus*, one of the Perch family, is hermaphrodite and self-impregnating,

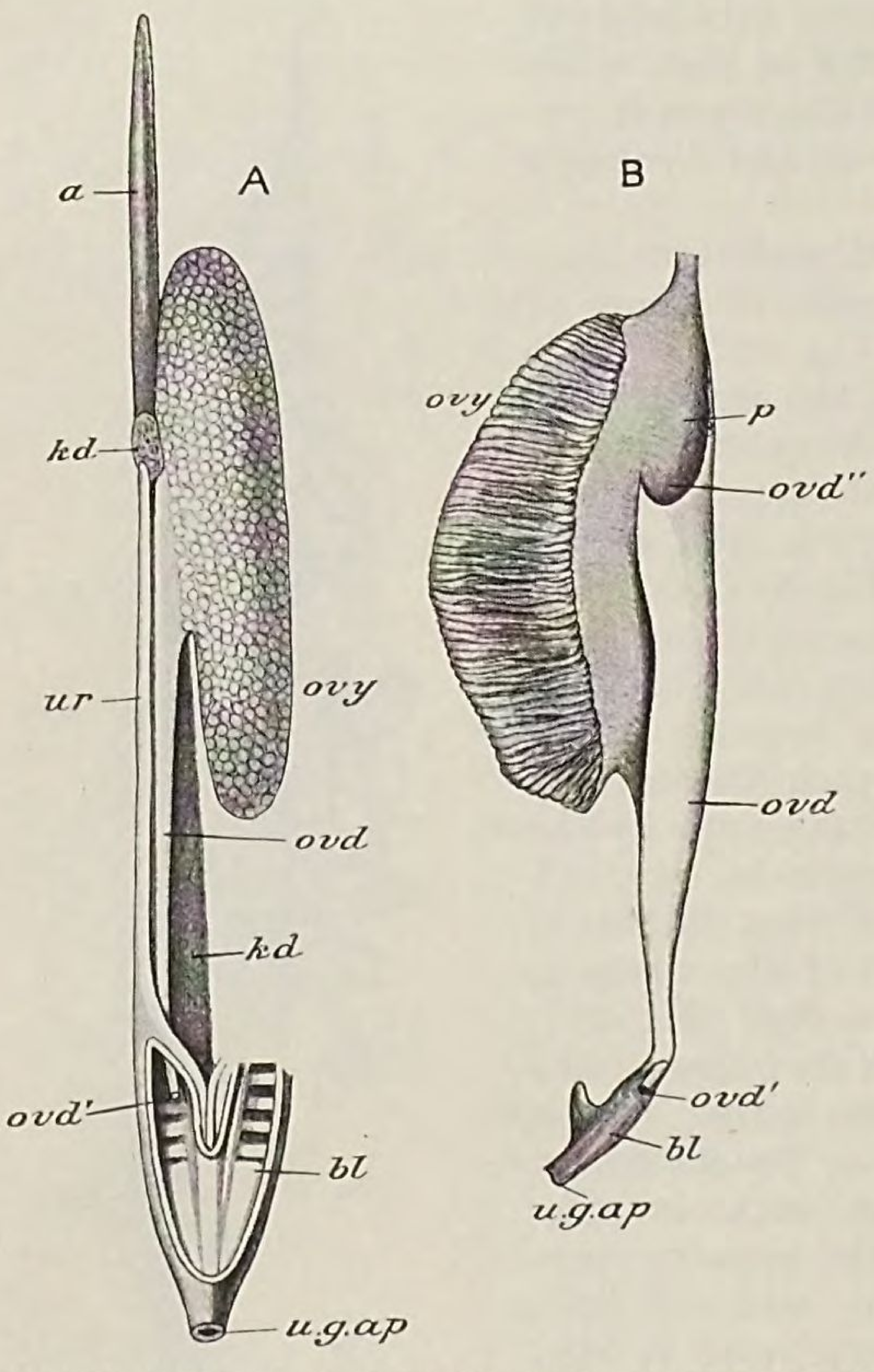


FIG. 847.—Female organs of **Lepidosteus** (A) and **Amia** (B). *a*, degenerate anterior portion of kidney; *bl.* bladder; *kd.* kidney; *ovd.* oviduct; *ovd.'* aperture of oviduct into bladder; *ovd.''* peritoneal aperture; *ovy.* ovary; *p.* peritoneum; *u.g. ap.* urino-genital aperture; *ur.* ureter. (A, after Balfour and Parker; B, after Huxley.)

and there are many well-known species, such as the Cod and the Herring, which exhibit the hermaphrodite condition as an occasional variation.

Reproduction and Development.—Most Teleostomi are oviparous, the eggs being impregnated after they are laid, but in some Teleostei, such as the Viviparous Blenny (*Zoarces*), internal impregnation takes place; the young are developed in the hollow ovary and are brought forth alive. Many instances of parental care of the young are known, the most familiar being that of the male Stickleback (*Gasterosteus*), which constructs a nest of weeds, fastened together by a glutinous secretion of the kidneys, and jealously guards the developing young. In the Sea-horse (*Hippocampus*) and the Pipe-fish (*Syngnathus*) the young are developed in a pouch (Fig. 832, *brd. p.*) on the abdomen of the male. In the Siluroid *Aspredo* the eggs are pressed into the soft spongy skin of the belly and thus carried about by the parent. The ova are always small as compared with those of Elasmobranchs, never exceeding 5 to 10 mm. in diameter, and being usually much smaller. They are rarely protected by an egg-shell. They are produced in immense numbers, a single female sometimes laying several millions: in such cases the mortality among the unprotected embryos and young is immense. The eggs may be *pelagic*, *i.e.* so light as to float when laid, as in the Cod, Haddock, Turbot, Sole, &c., or *demersal*, *i.e.* so heavy as to sink to the bottom, as in the Herring, Salmon, Trout, &c. In some cases they become cemented to the surface of a rock.

In all the Ganoids hitherto investigated segmentation is complete, but very unequal (Fig. 848): the megameres are immense as compared with the micromeres, and the process may be said to be intermediate between the holoblastic and meroblastic types. In Teleostei, on the other hand, segmentation is always partial and discoidal. The general features of development are much the same as in the Trout, except that in the Sturgeon there is an open medullary groove. There is frequently a metamorphosis: in Lepidosteus, for instance, the newly hatched young is provided with a sucking-disc, and the proportions of the head are quite different from those of the adult. In the larval Sturgeon provisional teeth are present, and in many Teleostei the young differ from the adult in the presence of large spines, which probably, like the spines in the zoæa-stage of some Crustacea, serve a defensive purpose. The larvæ of Eels are

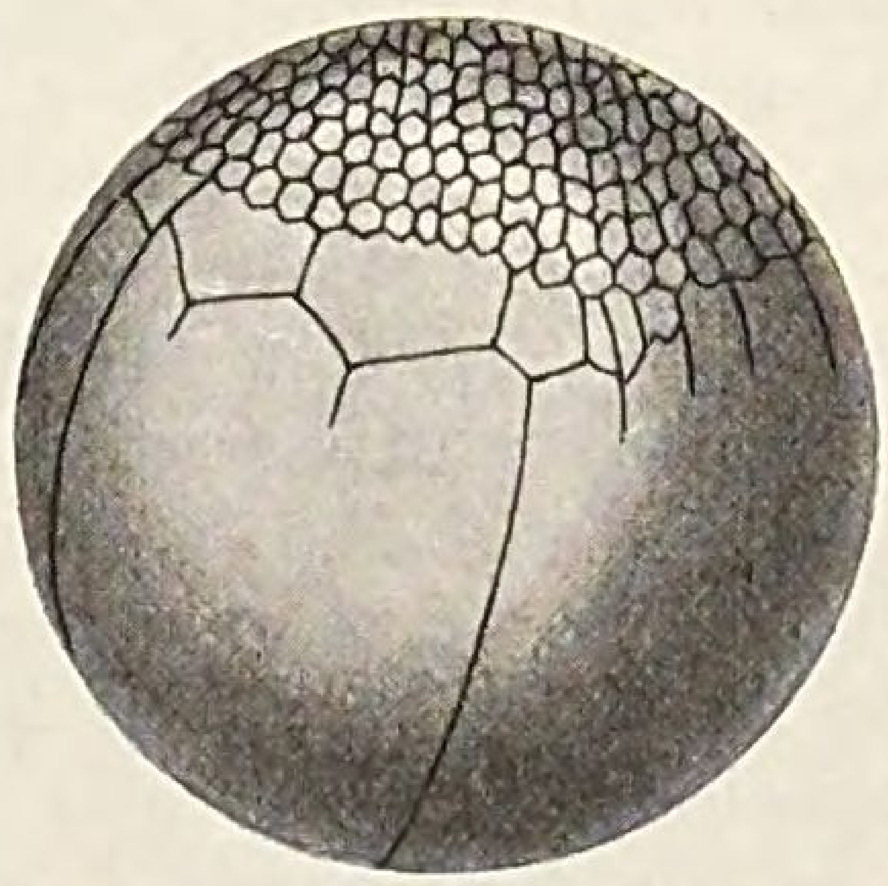


FIG. 848.—Segmentation in **Lepidosteus.** (After Balfour and Parker.)

strongly compressed, perfectly transparent, and have colourless blood. They are sometimes known as "Glass-fish," and were formerly placed in the genus *Leptocephalus*, their real nature being unknown. The Crossopterygii (or at least Polypterus) are unique

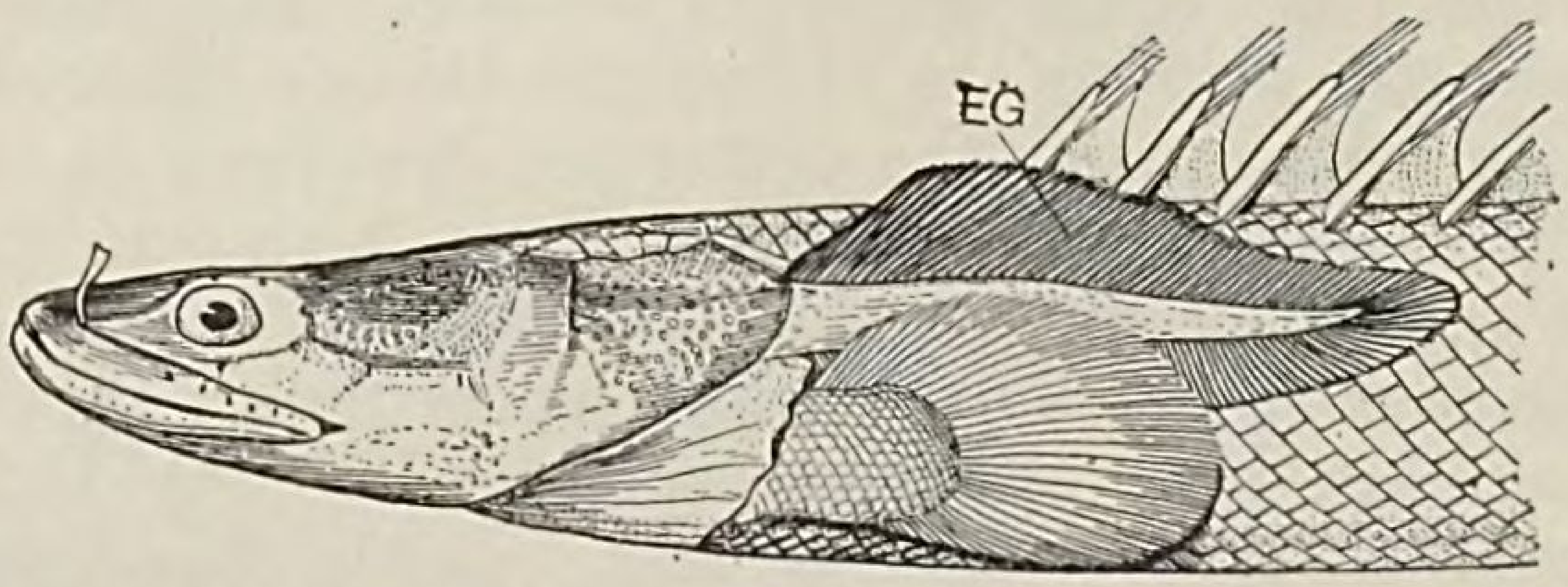


FIG. 849.—**Polypterus bichir.** Head of advanced larva; E. G. external gill. (From Dean, after Steindachner.)

in the sub-class in possessing, on each side, a single *external gill*, as in Dipnoi and Amphibia (*vide infra*).

The **Geographical Distribution** of the Ganoid Teleostomi is curiously limited: they are all essentially fresh-water forms—although some Sturgeons are found in the sea—and are almost exclusively inhabitants of the Northern Hemisphere, and especially of the Holarctic Region. The Chondrostei occur in the rivers of Europe, Asia, and North America: one genus of Sturgeons (*Scaphirhynchus*) lives in the Mississippi and in the rivers of Central Asia, but not in the intermediate regions: in the same way *Polyodon* is found only in the Mississippi, while the closely-allied *Psephurus* is found in the Yangtse-kiang and Hoangho—a striking instance of discontinuous distribution. Amia is found in the fresh waters of the United States; Lepidosteus extends also into Central America and Cuba. Polypterus lives in the Upper Nile and some other tropical African rivers; Calamoichthys in the Old Calabar River.

Among Teleostei the Physostomi are largely, though not exclusively, fresh-water Fish; the Carps, Eels, Salmonoids, and Siluroids are important examples. The Acanthopteri, Pharyngognathi, and Anacanthini are mostly marine, some being inhabitants of the shores, some pelagic, some abyssal, extending to a depth of nearly 3,000 fathoms. As we have seen, many species are practically terrestrial. All the sub-orders are universally distributed, so that we have to descend to families before meeting with any important facts in geographical distribution.

The **Distribution in Time** of the Teleostomi is interesting as showing the gradual replacement of the lower or more generalised members of a group by the higher or more specialised forms. During the whole of the Palæozoic and the greater part of the Mesozoic era the three orders of Ganoids, to-day small and isolated groups, formed the whole of the Teleostomian fauna,

and it is not until the Cretaceous period that the Teleostei, the present dominant order, make their appearance. From the Cretaceous onwards the Ganoids undergo a progressive diminution in numbers, genus after genus and family after family becoming extinct, while a corresponding increase takes place in all the sub-orders of Teleostei.

The Crossopterygii make their first appearance in the Devonian period, and, between that period and the Cretaceous, include six families and a large number of genera and species. They exhibit (Fig. 850) a very considerable range of variation in external

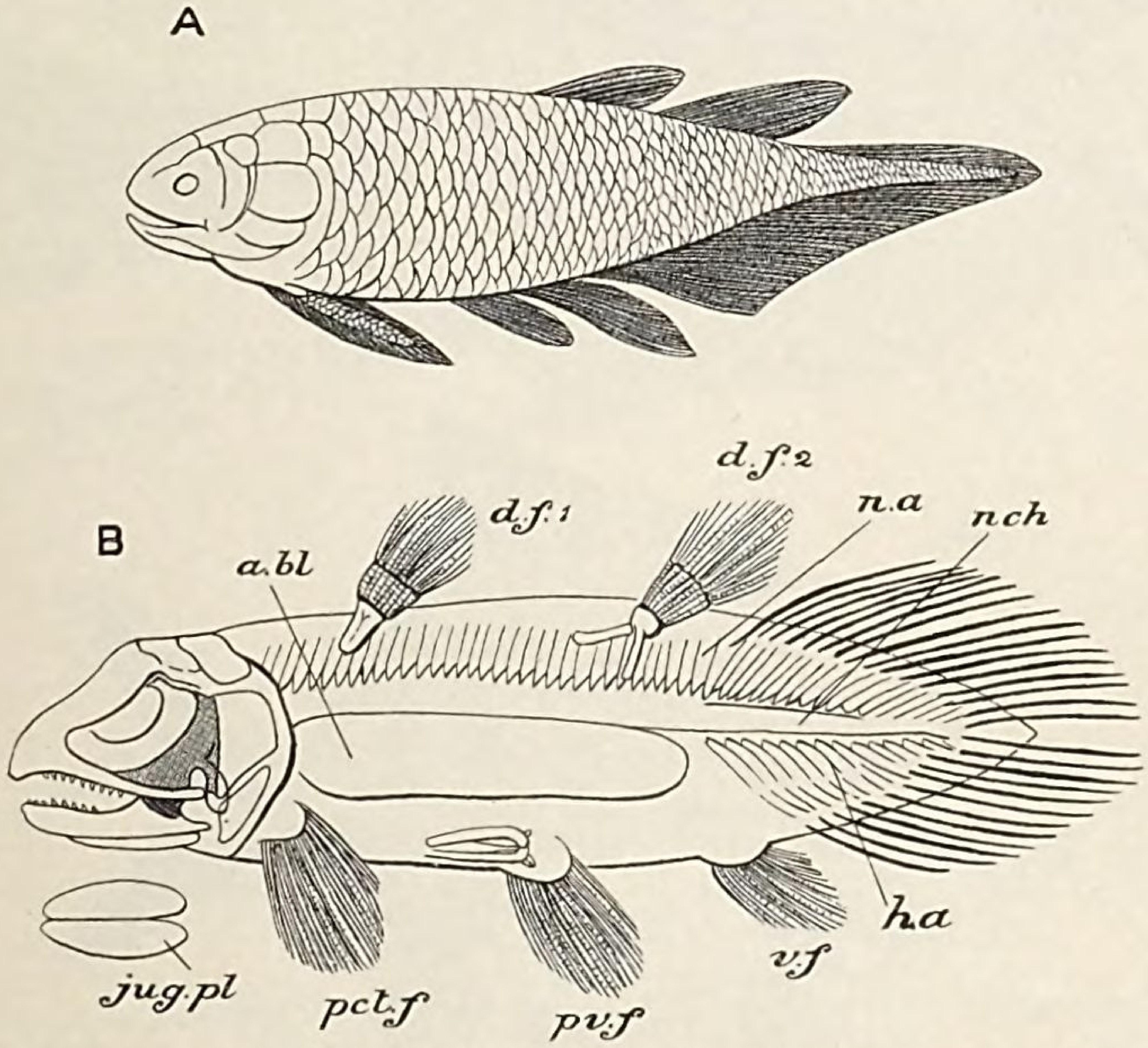


FIG. 850.—A, restoration of **Glyptolepis** (Devonian); B, **Macropoma mantelli** (Cretaceous). *a. bl.* ossified air-bladder; *d. f. 1*, *d. f. 2*, dorsal fins; *h. a.* hæmal arches; *jug. pl.* jugular plates; *n. a.* neural arches; *nch.* position of notochord; *pct. f.* pectoral fin; *pv. f.* pelvic fin; *v. f.* ventral fin. (From Nicholson and Lydekker.)

and internal characters. There are usually two dorsal fins, the tail may be diphycercal or heterocercal, the scales rhomboid or cycloid. In some genera, also, there was a persistent notochord (*B. nch.*), the fossils showing well-preserved neural and hæmal arches, but no signs of centra. In many cases the interspinous bones or proximal pterygiophores of the dorsal fins are fused into a single basal bone. All agree in the possession of lobed fins, the basal lobe is sometimes so long as to approach the type of structure we shall find to characterise the Dipnoi (*vide infra*).

The Chondrostei are also largely represented, from the Devonian upwards, and include a great variety of forms, many of which,

apart from the heterocercal tail, have a strong external resemblance to Teleostei (Fig. 851). Some have the characteristic spindle-form of strong-swimming Fishes (A), others the high compressed form of such shore-fishes as the Reef-fishes (B). Scutes are present in some species, rhomboid scales in others, and in one genus the greater part of the body is covered by

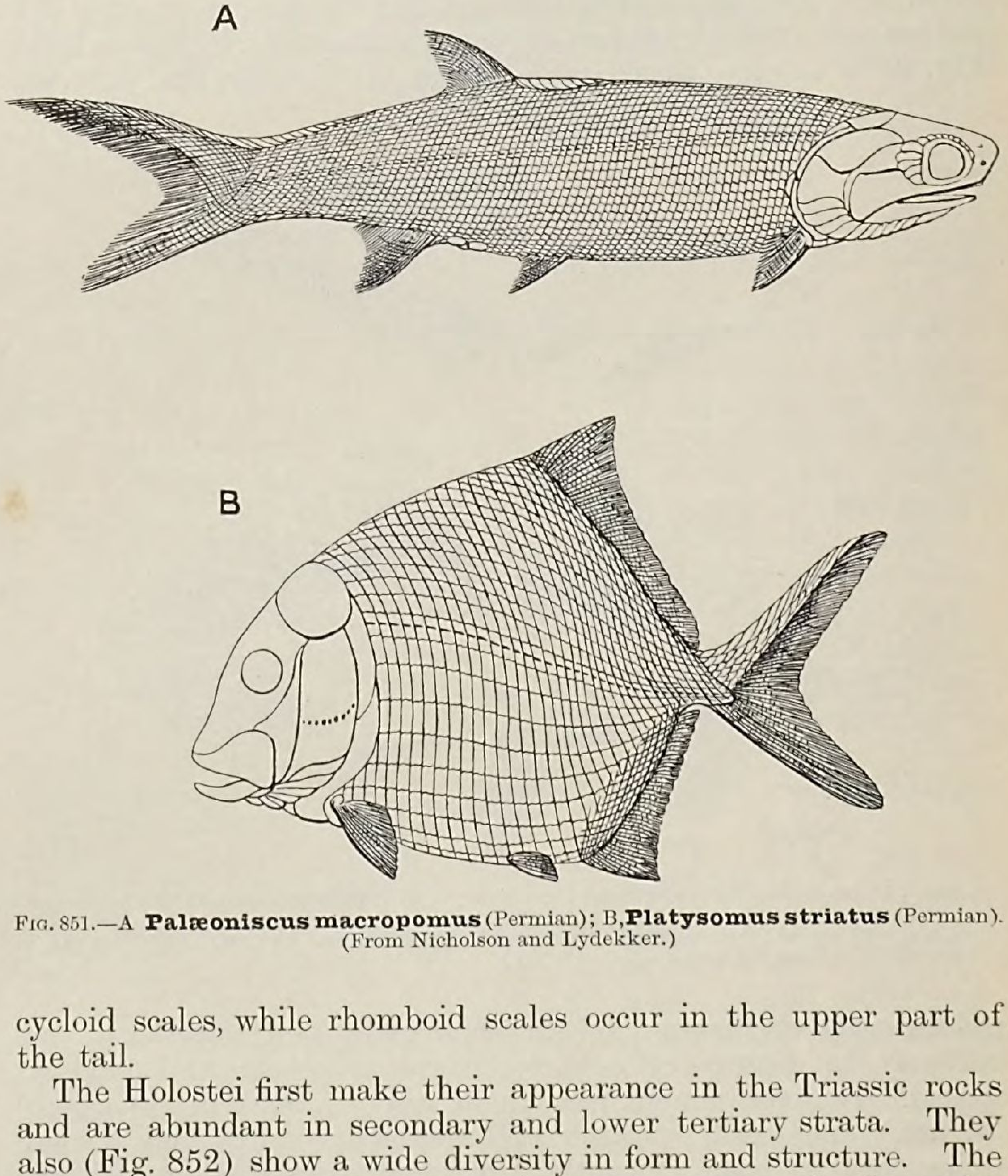


FIG. 851.—A **Palæoniscus macropomus** (Permian); B, **Platysomus striatus** (Permian). (From Nicholson and Lydekker.)

cycloid scales, while rhomboid scales occur in the upper part of the tail.

The Holostei first make their appearance in the Triassic rocks and are abundant in secondary and lower tertiary strata. They also (Fig. 852) show a wide diversity in form and structure. The body may be spindle-shaped or high and compressed; the scales may be rhomboid or cycloid, or may exhibit every gradation from rhomboid to cycloid in passing from the trunk to the tail of one and the same Fish; the teeth may be sharp and conical, or blunt, rounded, and adapted for crushing. A persistent notochord is present in some species, a well-ossified vertebral column in others.

We see, then, that all the orders of Ganoids, during the period of their prime, branched out into diverse forms, adapted to different environments, and often resembling, in a remarkable manner, the divergent forms of Teleostei which fill similar positions at the present day.

The Teleostei first appear in the Cretaceous rocks, where many existing families are represented. From this period onwards the three Ganoid orders undergo a progressive diminution in the

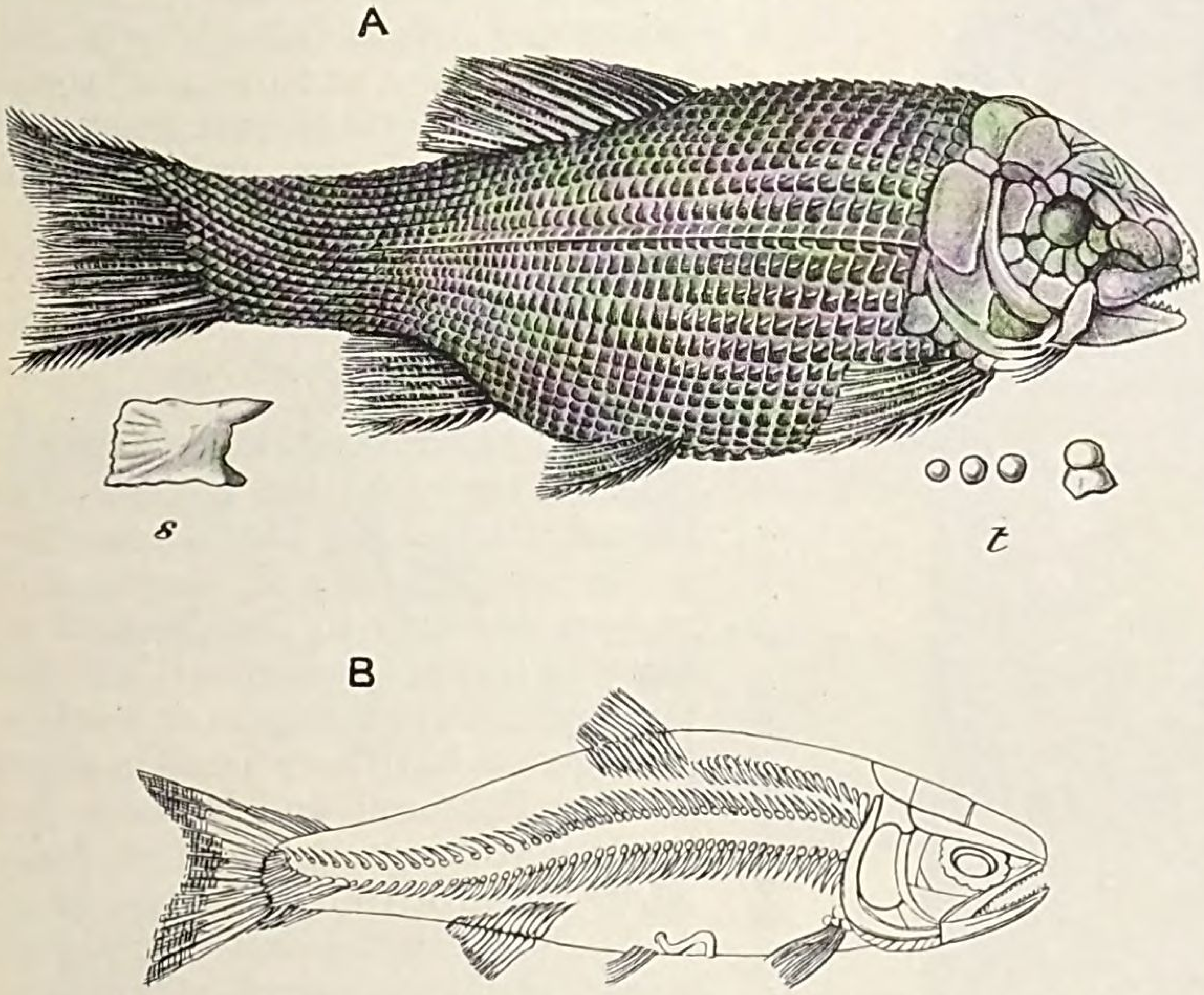


FIG. 852.—A, **Lepidotus maximus** (Jurassic). *s.* scale ; *t.* teeth. B, **Caturus furcatus** (Jurassic). (From Nicholson and Lydekker.)

number of families, genera, and species, their places being taken by the more highly differentiated Teleostei, until, at the present day, as we have seen, they are reduced to a few scattered forms, mostly confined to fresh waters.

Sub-class V.—The Dipnoi.

The Dipnoi or Lung-fishes, comprising as their living representatives only the Queensland *Ceratodus* or "Burnett Salmon," and the Mud-fishes (*Protopterus* and *Lepidosiren*) of certain South African and South American rivers, are fishes of such well-marked and special features that by some zoologists they are separated from the true Fishes and regarded as constituting a separate class

of Vertebrates. One of their peculiar features is indicated by the name *Dipnoi.* Not only do these animals breathe by means of gills, like ordinary Fishes, but they have a highly developed apparatus for the respiration of air—a lung or lungs—with an arrangement of the circulation co-ordinated with this. They have bony scales and dermal fin-rays, but the paired fins, unlike those of any other fishes, with the exception of certain extinct Elasmobranchs, are constructed on the type of the archipterygium (see p. 155).


FIG. 853.—**Ceratodus Forsteri.** Reduced. (From Dean, after Günther.)

1. Example of the Class—*Ceratodus Forsteri.*

The Ceratodus or "Burnett Salmon" (Fig. 853) is by far the largest of the Dipnoi, attaining a length sometimes of four or five feet. It occurs at the present day only in the Burnett and Mary Rivers in Queensland, but fossil teeth referred to the same or nearly related genera have been found in abundance in Palæozoic and Mesozoic beds in Europe, America, the East Indies, Africa, and Australia. It lives in still pools in which the water in the dry season becomes extremely stagnant and overladen with decomposing vegetable matter; and it is only by rising to the surface occasionally, and taking air into its lung, that it is enabled to obtain sufficient oxygen for purposes of respiration. Its food consists of such small animals as live among the water-plants and decaying leaves, and in order to obtain a sufficient amount of such food it swallows relatively large quantities of vegetable matter, which passes with little or no alteration through its enteric canal.

External Characters.—The *body* is fish-like (Fig. 853) with a diphycercal caudal fin. The surface is covered with very large imbricated cycloid scales, somewhat

smaller towards the tail. The limbs have a characteristic shape, being in the form of two pairs of elongated, leaf-like, pointed paddles. The mouth is situated on the ventral surface of the head, close to the anterior extremity of the snout. The external nares differ from those of other Vertebrates in being situated immediately outside the aperture of the mouth, enclosed within the upper lip. A pair of internal nares opens not far behind them into the anterior part of the mouth cavity. At the root of the tail is the cloacal aperture. There is an operculum similar to that of the Teleostomi, with a single slit-like branchial aperture behind it.

Endoskeleton.—The *spinal column* (Fig. 854) is represented by a persistent notochord enclosed in a sheath without any trace of

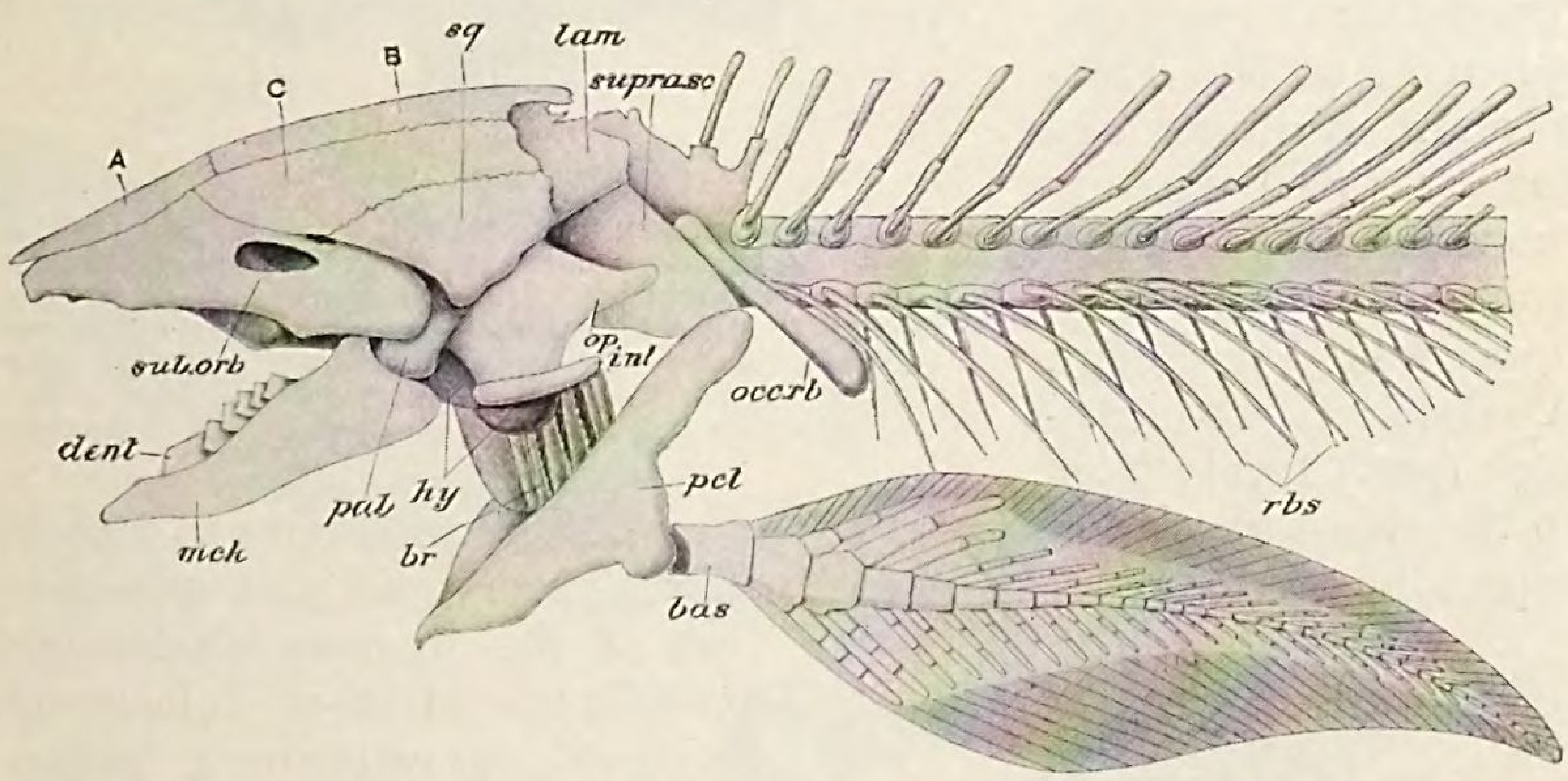


FIG. 854.—**Ceratodus Forsteri.** Lateral view of the anterior portion of the skeleton. *A*, anterior median membrane-bone of the roof of the skull. *B*, posterior median membrane-bone. *bas.* basal cartilage of the pectoral fin; *br.* branchial arches; *int.* inter-operculum; *lam.* plate overhanging branchial region; *mck.* Meckel's cartilage; *occ. rb.* occipital rib; *op.* operculum; *pal.* palato-quadrate; *pct.* pectoral arch; *rbs.* ribs; *sub. orb.* sub-orbital bones; *sq.* squamosal; *supra-sc.* supra-scapula.

separate vertebræ, except in the caudal region, the segmentation being indicated by the metamerically arranged neural arches and ribs. Each neural arch, composed partly of cartilage, partly of bone, bears on its summit a slender rod composed of three segments representing a neural spine, a basal cartilage, and a radial cartilage—the two last extending into the unpaired fin. In the caudal region the hæmal arches present a similar arrangement. The most anterior of the vertebræ are coalescent with one another and with the skull. At the sides of the præ-caudal region are a series of rod-like cartilages of the nature of ribs.

The *skull* (Figs. 854, 855 and 856) consists of an undivided mass of cartilage, narrowest between the orbits and broadening before and behind; posteriorly it is prolonged into a plate (*lam.*) overhanging

the branchial region Imbedded in the cartilage of the posterior part are a small pair of exoccipital ossifications. On the upper surface two unpaired (*A* and *B*) and four paired (*C* and *Sq*) membrane-bones overlie the cartilage; and on the ventral surface is a large membrane-bone (Fig. 856, *P. sph.*) representing the parasphenoid of the Teleostomi. Rudimentary vomers (*Vo.*) support the vomerine teeth In front is a pair of small upper labial cartilages. A palatoquadrate cartilage (*pal.*) firmly fixed to the side-wall gives support to the mandible, and seems to contain representatives, not only of the palatine, pterygoid and quadrate, but of the hyomandibular and symplectic of the Teleostomi. In front it contains a palato-pterygoid ossification. Behind it a small cartilage immovably fixed to the side-wall of the skull is probably the opercular cartilage. One of the two lateral membrane-bones (*Sq*) situated over the palato-quadrate is the squamosal. Opercular (*op.*) and interopercular (*int.*) bones support the operculum. The hyoid (*hy.*) and branchial arches (*br.*) are cartilaginous. Of the latter, four are completely developed, each consisting of a dorsal and a ventral cartilage; a fifth is represented by a rudiment attached to the fourth.

The pectoral arch (Fig. 854, *pct.*) is a stout cartilage with a

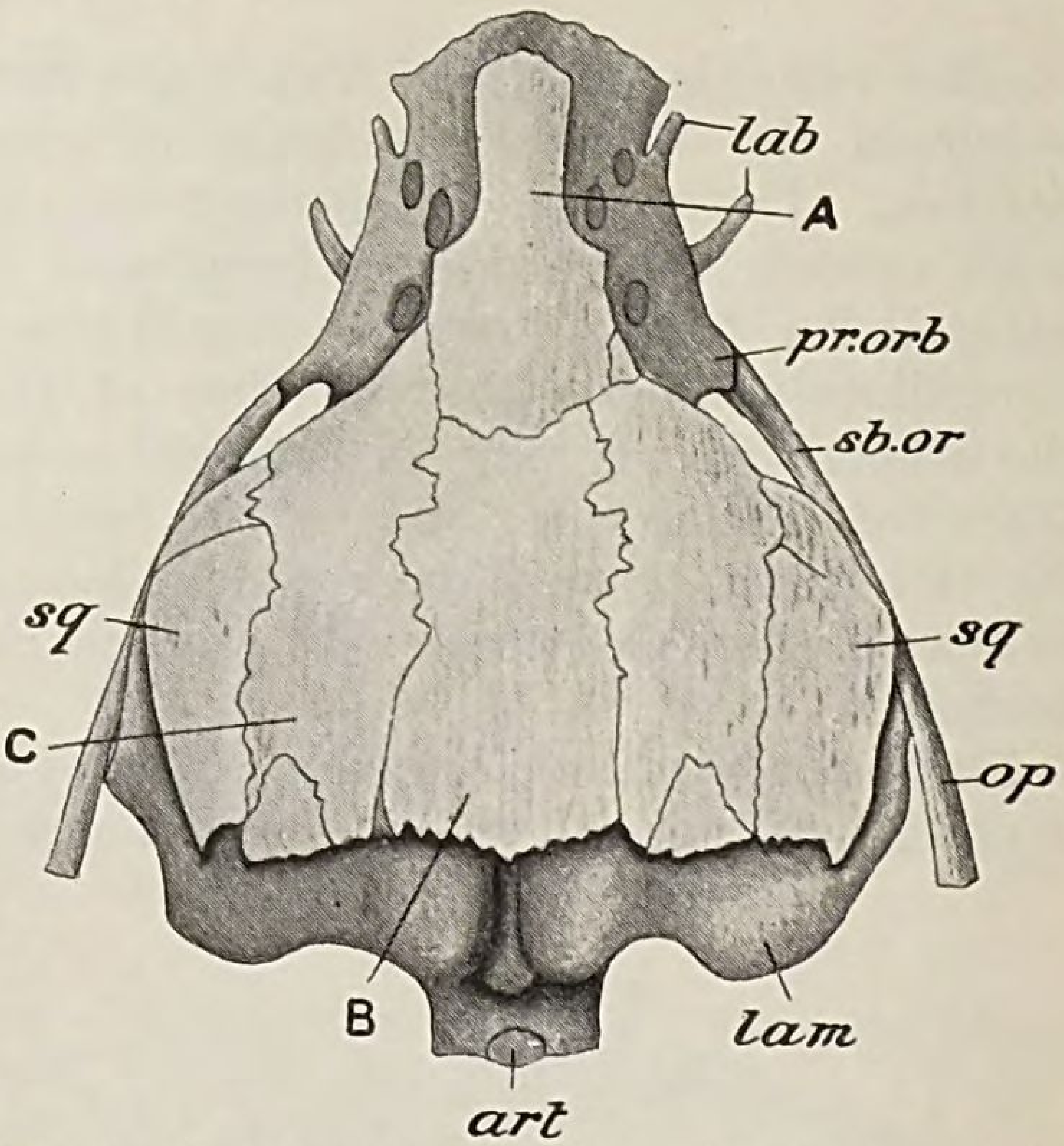


FIG. 855.—**Ceratodus Forsteri.** Dorsal view of the skull. *A*, anterior median membrane-bone; *art.* articular surface for second fin-ray; *B*, posterior median membrane-bone; *C*, inner lateral membrane-bone; *lab.* labia cartilages; *lam.* process projecting over gills; *op.* operculum; *pr.orb.* præ-orbital process of chondrocranium; *sb. orb.* sub-orbital bones *sq.* squamosal. (After Huxley.)

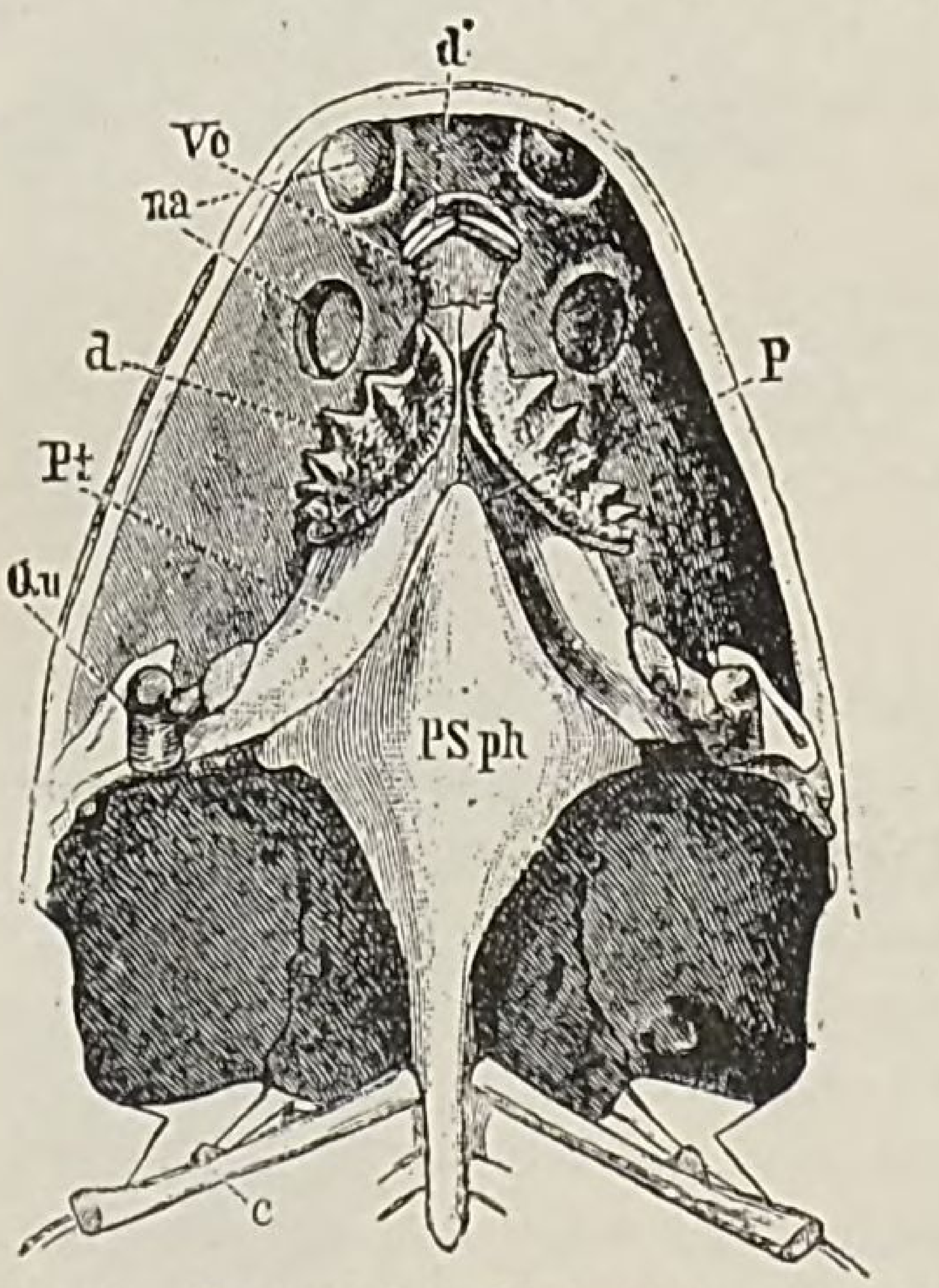


FIG. 856.—**Ceratodus Forsteri.** Ventral view of the skull. *c*, occipital rib; *d*, palatine teeth; *d'*, vomerine teeth; *na.* anterior and posterior nares; *P.* palatine region of palato-pterygoid; *P.sph.* parasphenoid; *Pt.* pterygoid; *Qu.* quadrate region; *Vo.* vomer. (From Dean, after Günther.)

pair of investing bones. The skeleton of the pectoral fin consists of a stout basal cartilage (*bas.*), an elongated tapering central axis made up of a number of short cartilaginous segments, and two rows of jointed cartilaginous rays extending out on either side of the axis so as to support the expanse of the fin. The pelvic arch is a single cartilage, produced forwards into an elongated rod-like process. The skeleton of the pelvic fin (Fig. 857) is similar to that of the pectoral.

Digestive Organs.—The *teeth* (Fig. 856) are of a remarkable and characteristic shape. There are two pairs of large compound teeth of similar character, one pair (*d.*) on the roof of the mouth (palato-pterygoid region) and the other on the lower jaw. Each is a curved plate with the convex border, which is directed inwards and somewhat backwards, entire, while the concave border presents a series of six or seven

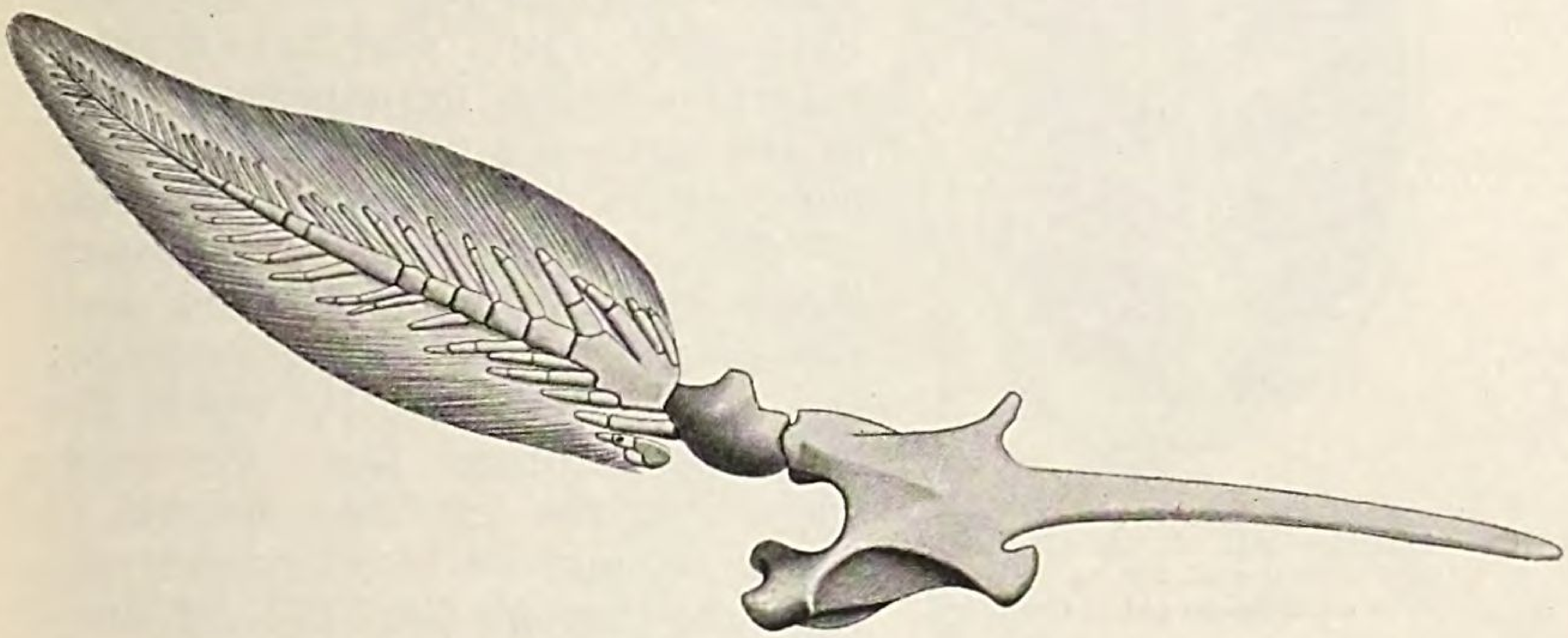


FIG. 857.—**Ceratodus Forsteri.** Pelvic arch and skeleton of pelvic fin. (After Günther.

bluntly pointed projections or cusps. In addition to these there are, in front of the palatine pair, a pair of much smaller, simple, somewhat chisel-like *vomerine* teeth (*d′*) placed close together and directed vertically.

In the *enteric canal* the chief feature of special interest is the presence, throughout the length of the intestine, of a spiral valve similar to that of the Elasmobranchs and Ganoids. The rectum opens into a small cloaca. A pair of abdominal pores open just behind this.

Organs of Respiration.—Ceratodus combines aquatic respiration by means of gills similar to those of true fishes, with aerial respiration by means of a lung.

There are four pairs of *gills*, each consisting of a double row of gill-filaments supported on the branchial arches. A rudimentary hyoidean gill or *pseudobranch* is present as well. The lung (Fig. 858) is an elongated median sac connected with the ventral wall of the

pharynx by a slit-like aperture, the glottis. Its internal surface is sacculated, and a regularly-arranged series of blind pouches open out of the main central cavity. This *lung* of Ceratodus corresponds morphologically to the air-bladder of Ganoids and Teleosts, but differs from it in its blood-supply, and consequently in its function, being supplied with venous blood by a special *pulmonary artery* and acting as an important organ of respiration.

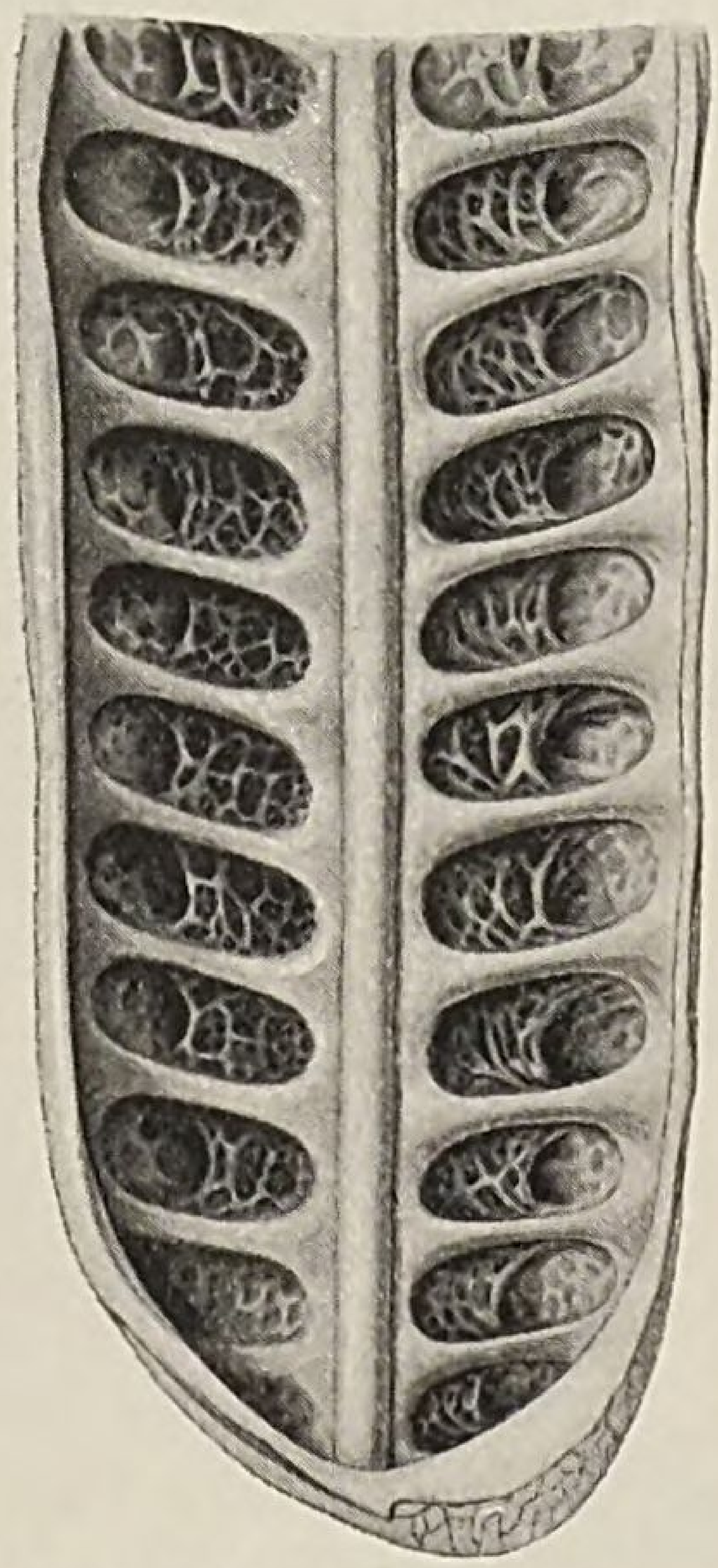


Fig. 858.—**Ceratodus Forsteri.** Posterior half of the lung with the ventral wall slit up so as to show the interior. (After Günther.)

Blood Vascular System.—Co-ordinated with the existence of a lung and distinct pulmonary circulation is a complication in the structure of the heart. The *sinus venosus* is imperfectly divided into two parts, and the cavity of the auricle is divided into two by an incomplete septum in the form of a ridge. The venous blood enters the right-hand division of the sinus venosus and passes thence through the right-hand division of the auricle to the ventricle; the pulmonary vein, by which the blood is returned from the lung, opens into the left-hand division of the sinus, and its blood reaches the ventricle through the left-hand division of the auricle. There are no auriculo-ventricular valves guarding the opening between the auricle and the ventricle. A contractile conus arteriosus is present, and has a remarkable spirally-twisted form; in its interior are eight transverse rows of valves, and its cavity is divided imperfectly by means of an incomplete longitudinal septum.

The blood-vessels (Fig. 859) present an arrangement which is intermediate in some respects between that which has been already described as observable in the Elasmobranchs and that which will be found to characterise the Amphibia. The four afferent branchial arteries (*aff.*) take their origin close together, immediately in front of the conus, so that a ventral aorta can hardly be said to exist. Each branchial arch has two efferent branchial arteries (*epi.*). A hyoid artery (*hy. art.*) is connected dorsally and ventrally with the most anterior of these. The eight efferent vessels unite in pairs to form four epibranchial arteries. The latter unite dorsally to form a main trunk, which combines with the corresponding trunk of the opposite side to form the median *dorsal aorta* (*d. a.*). The head is supplied by *carotid* branches

given off from the first epibranchial (*l. ant. car.* and *r. ant. car.*) and from the hyoidean arteries (*l. post. car.* and *r. post. car.*), and the latter also gives off a *lingual artery* to the tongue. From the last (fourth) epibranchial artery arises the pulmonary artery (*l. pul. art.* and *r. pul. art.*), carrying blood to the lung.

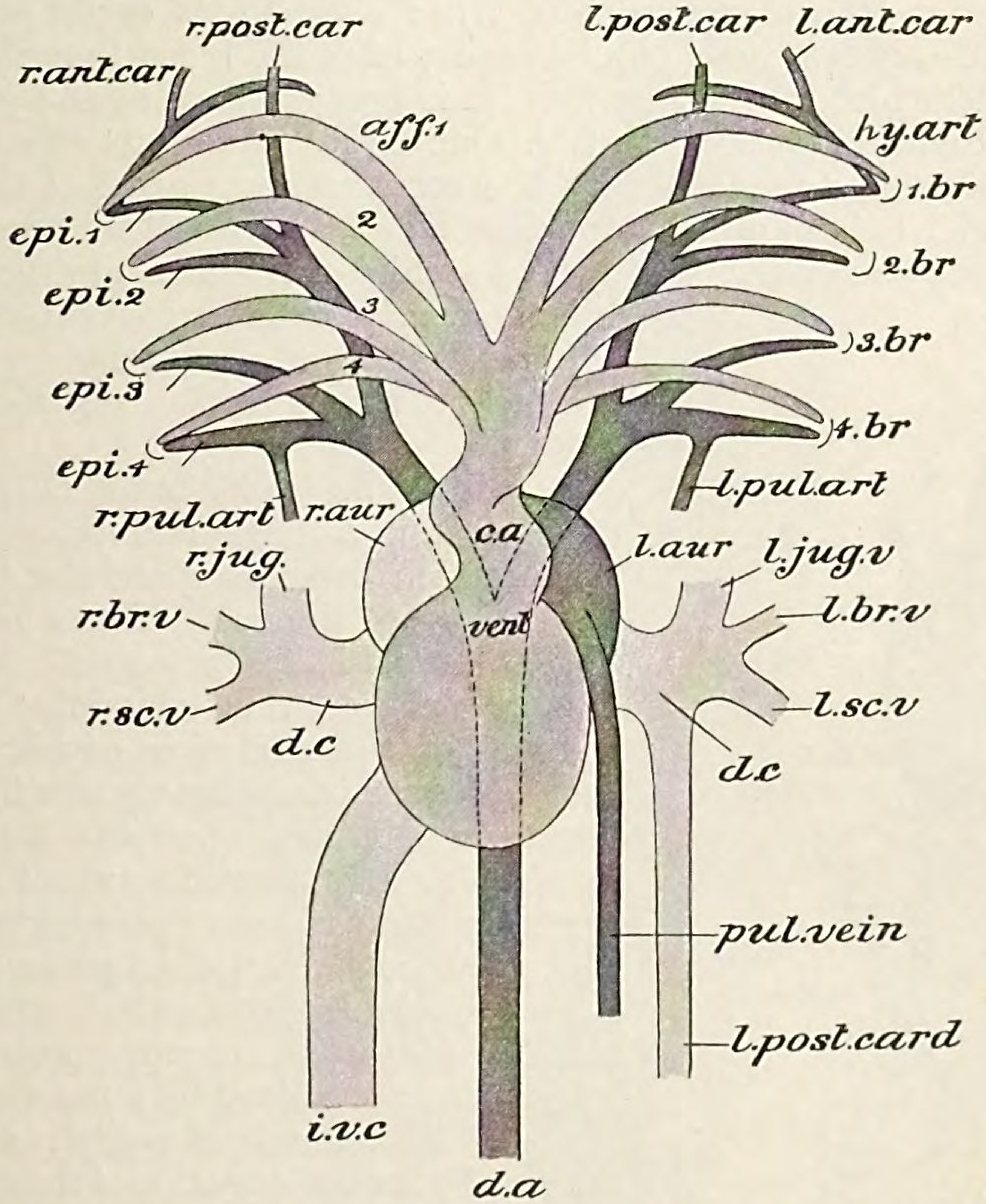


FIG. 859.—**Ceratodus Forsteri.** Diagrammatic view of the heart and main blood-vessel, as seen from the ventral surface. *aff.* 1, 2, 3, 4, afferent vessels; 1 *br*, 2 *br*, 3 *br*, 4 *br*, position of gills; *c. a.* conus arteriosus; *d. a.* dorsal aorta; *d. c.* ductus Cuvieri; *epi.* 1, *epi.* 2, *epi.* 3, *epi.* 4, efferent branchial arteries; *hy. art.* hyoidean artery; *i, v, c,* post-caval vein; *l. ant. car.* left anterior carotid artery; *l. aur.* left auricle; *l. br. v.* left branchial vein; *l. jug. v.* left jugular vein; *l. post. car.* left posterior carotid artery; *l. post. card.* left posterior cardinal vein *l. pul. art.* left pulmonary artery; *l. sc. v.* left sub-scapular vein; *r. ant. car.* right anterior carotid artery; *r. aur.* right auricle; *r. br. v.* right brachial vein; *r. jug. v.* right jugular vein; *r. post. car.* right posterior carotid; *r. pul. art.* right pulmonary artery; *r. sc. v.* right sub-scapular vein; *vent.* ventricle. (After Baldwin Spencer.)

There are two *ductûs Cuvieri* (*d. c.*), as in the Dog-fish (p. 146). The right ductus is formed by the union of *jugular* (*l. jug. v.* and *r. jug. v.*), *brachial* (*l. br. v.* and *r. br. v.*), and *subscapular* veins (*l. sc. v.* and *r. sc. v.*). The left receives in addition a left *posterior cardinal vein* (*l. post. card.*). A large *lateral cutaneous* vein running superficially along the side of the body opens into the subscapular.

A large *post-caval vein* (*i. v. c.*) brings back the greater portion of the blood from the posterior parts of the body; it is situated somewhat to the right of the middle line, and opens into the sinus venosus between the two *hepatic veins*. The post caval is present in no other Fishes, but is universal in all the higher classes. Posteriorly the posterior cardinal and the post-caval are formed by the bifurcation of a median *caudal vein;* close to its origin each receives the *efferent renal veins* bringing back the blood from the kidney. The blood from the pelvic fin is brought back by an *iliac vein* which divides into two branches. One of these, running forwards and inwards, unites mesially with the corresponding vessel of the opposite side to form a median *abdominal vein*—a vessel not present in the Fishes, but universal in the Amphibia; it opens into the sinus venosus. The other branch is the *renal portal* vein; after receiving tributaries from the posterior region of the body it passes to the corresponding kidney.[1]

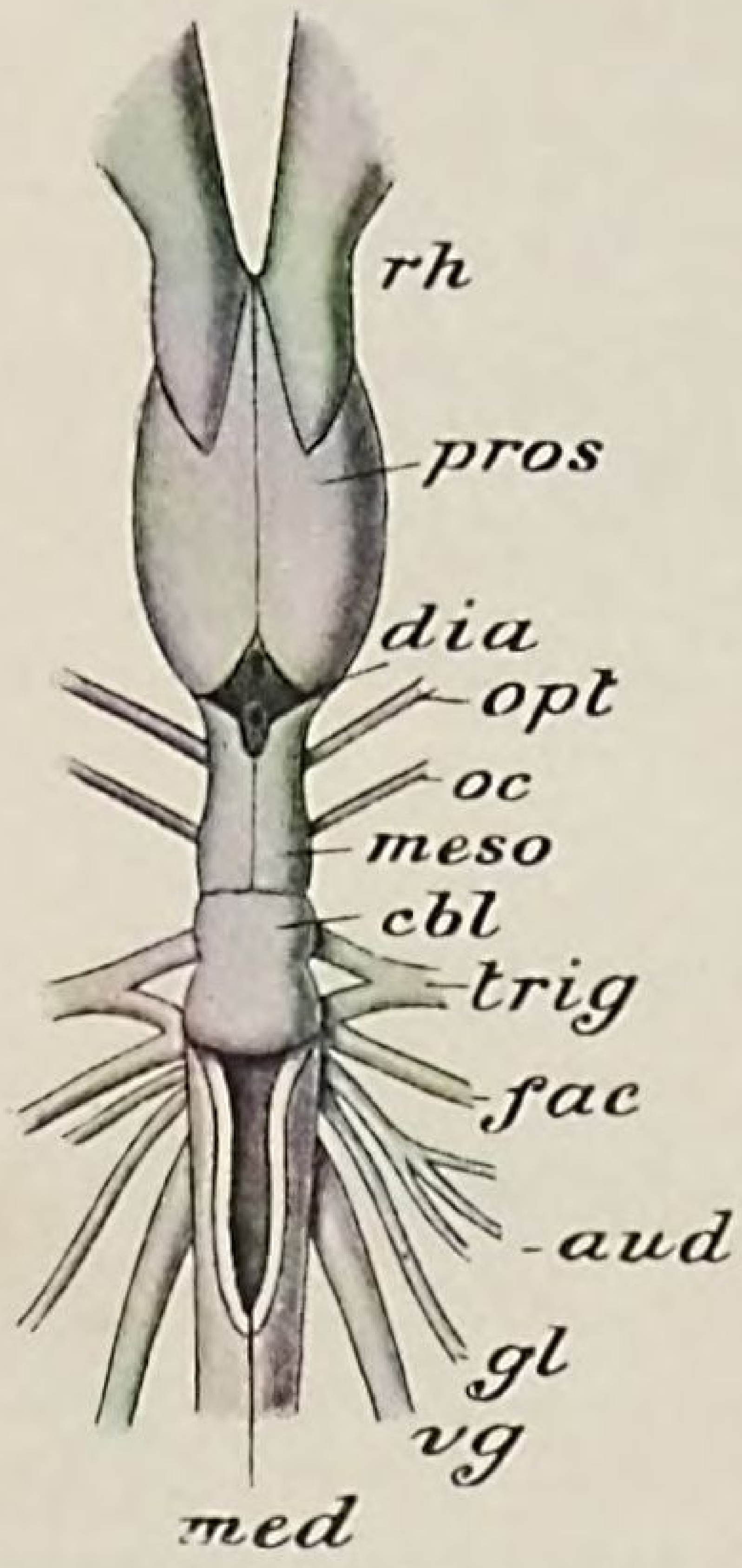


FIG. 860.—Brain of **Ceratodus Forsteri,** dorsal view. *aud.* auditory nerve; *cbl.* cerebellum; *fac.* facial nerve; *gl.* glosso-pharyngeal; *med.* medulla oblongata; *mes.* mesencephalon; *oc.* oculo-motor nerve; *opt.* optic nerve; *pros.* prosencephalon; *rh.* rhinencephalon; *vg.* vagus nerve. (Chiefly after Sanders.)

Brain.—The whole brain (Fig. 860) is enclosed in a tough and thick membrane, which becomes glandular in two positions—on the roof of the diacœle and on that of the metacœle. In the former position this glandular development of the enclosing membrane or choroid plexus passes downwards into the diacœle and is developed into a spongy mass which is prolonged forwards to the anterior end of the prosencephalon. The prosencephalon (*pros.*) presents two elongated hemispheres, which are completely separated except posteriorly, where they are united by a narrow commissure. The contained cavity is divided into two by the prolongation of the choroid plexus already referred to. The nervous wall of the hemisphere is very thin and is incomplete dorsally and internally. There is a pair of large olfactory lobes (*rh.*), each with its cavity or rhinocœle.

The pineal body is situated on the summit of a conical membranous cap on the roof of the third ventricle. The infundibulum developes a pair of lobi inferiores. The mesencephalon (*meso.*) is bilobed, but the division is not strongly pronounced. The cerebellum (*cbl.*) is very small,

[1] How far this arrangement combines fish-like and amphibian characters will be best understood at a later stage.

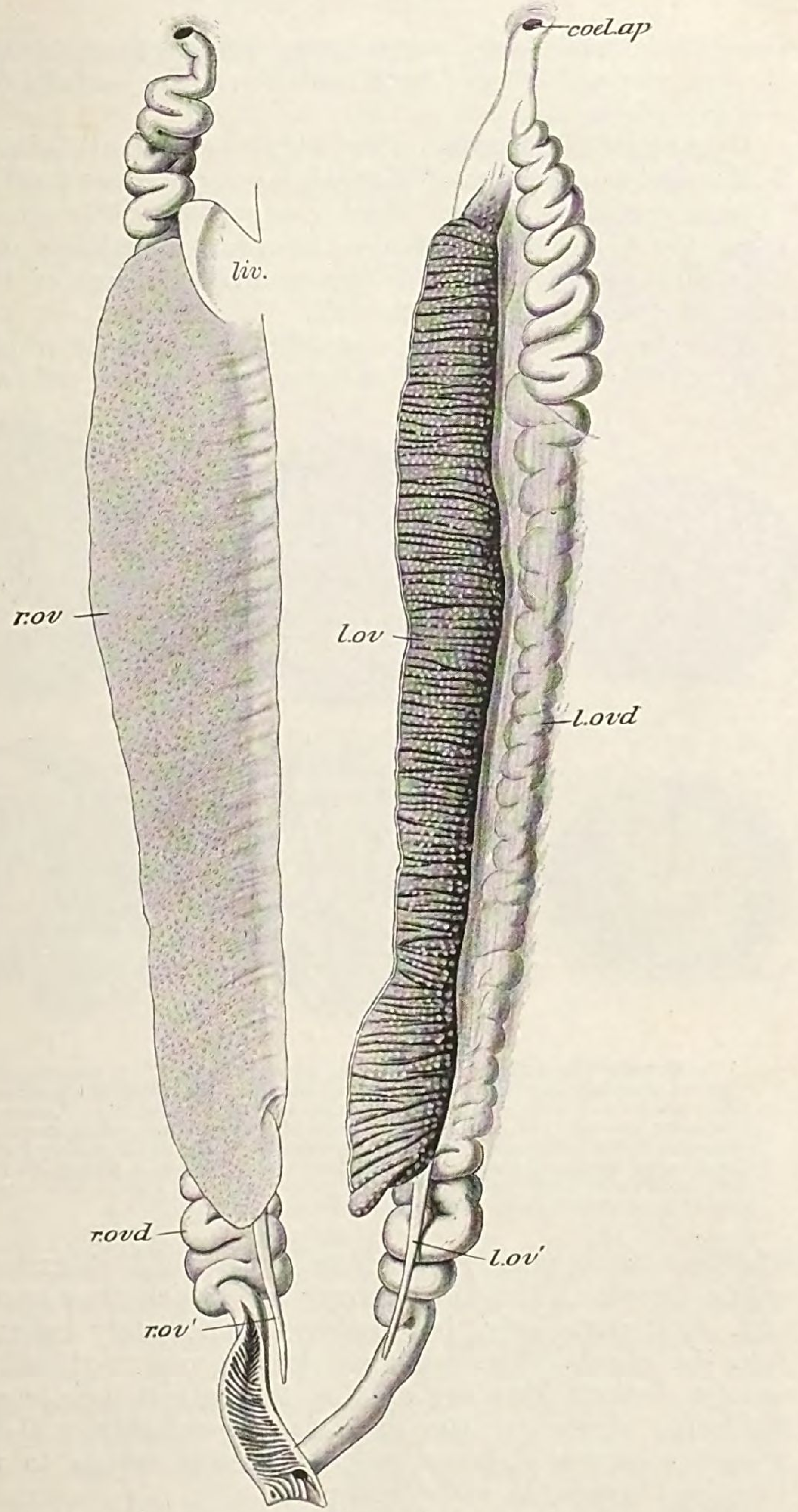


FIG. 861.—**Ceratodus Forsteri.** Reproductive organs of female; the inner surface of the right and the outer surface of the left ovary shown. *cœl. ap.* cœlomic aperture of oviduct; *liv.* portion of the liver; *l. ov.* left ovary; *l. ov'.* its posterior termination; *l. ovd.* left oviduct; *r. ov.* right ovary; *r. ov'.* its posterior termination; *r. ovd.* right oviduct. (After Günther.)

being little more than a transverse bridge of nerve-matter over the anterior end of the fourth ventricle. The medulla (*med.*) is of relatively large size.

Urinogenital Organs.—The *kidneys* are short, being confined to the posterior portion of the body-cavity, and are firmly attached to the ovaries or testes. Each has a thick-walled ureter which joins its fellow, the passages, however, remaining distinct to near the opening into the urinogenital division of the cloaca, when the right opens into the left.

There are two elongated *ovaries* (Fig. 861, *ov.*) which remain distinct throughout. The *oviducts* (*l. ovd.* and *r. ovd.*) are a pair

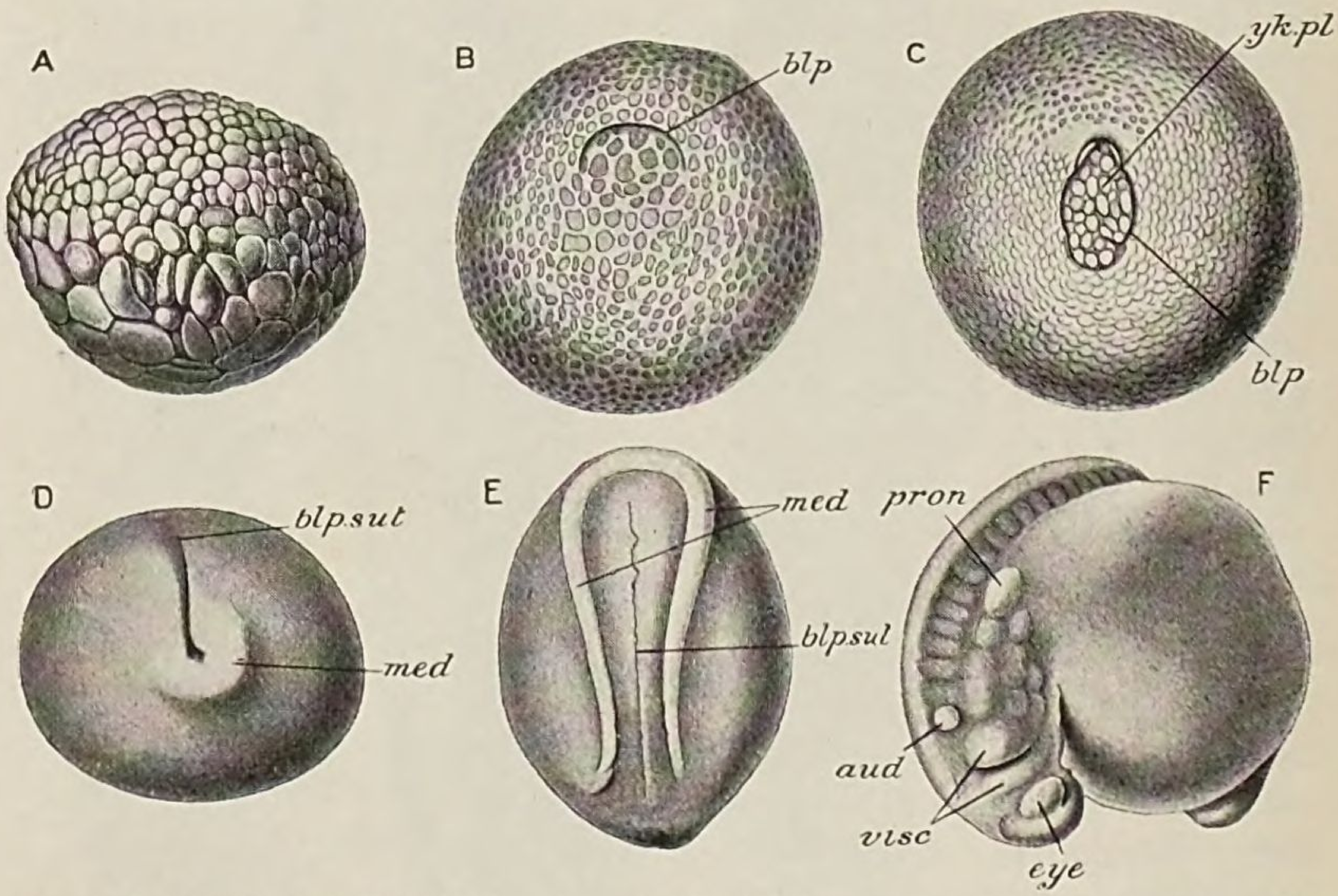


FIG. 862.—**Ceratodus Forsteri.** Stages in the development. *A*, lens-shaped blastula; *B*, stage with semicircular blastopore (*bl. p.*); *C*, later stage in which the blastopore (*bl. p.*) has taken the form of a ring-like groove enclosing the yolk-plug (*yk. pl.*); *D*, stage in which the blastopore (*blp. sut.*) has assumed the character of a longitudinal suture around which is the rudiment of the medullary folds (*med.*); *E*, stage in which the medullary folds (*med.*) have become well developed and enclose the blastopore reduced to a zig-zag slit; *F*, later stage with well-formed head with two visceral arches (*visc.*) and rudiments of eye (*eye*) and ear (*aud.*); *pron.* mesonephros. (After Semon.)

of thick-walled, greatly convoluted tubes which extend along the whole length of the body-cavity, into which they open in front (*cœl. ap.*); posteriorly they coalesce immediately before opening into the cloaca. The *testes* are long, compressed bodies which remain distinct from one another throughout their length. The Müllerian ducts in the male are remarkably well-developed. There is no vas deferens, and the sperms appear to reach the exterior through the abdominal pores.

In the early stages of its **development** (Fig. 862) Ceratodus exhibits resemblances, on the one hand, to *Petromyzon* (p. 126), and

on the other to the next class to be studied—the *Amphibia.* The ova become enclosed, while passing down the oviduct, in a gelatinous envelope which swells up considerably when it comes in contact with the water. At what stage fertilisation takes place is not exactly known. Segmentation is complete and unequal, and results in the formation of a lens-shaped blastula (*A*) with smaller cells on one of the convex surfaces (the future dorsal) and larger on the other (the future ventral). A blastopore (*bl. p.*) first appears on the ventral surface as a short transverse slit, which grows into a semicircle (*B*) or a horse-shoe. The free ends of this grow in towards one another and unite to enclose an irregularly circular or elliptical space filled in by a mass of large cells—the *yolk-plug* (*C yk. pl.*). Soon, however, this wide aperture becomes narrowed to a small longitudinal slit, the lips of the anterior part of which soon unite to form a longitudinal seam or suture, only the most posterior part remaining open (*D*). During its increase in size the blastopore has been growing over towards the dorsal side, and when its lips become united to form a suture it extends along the greater part of the dorsal surface. A pair of medullary folds appear at the sides of this (*E*) and are coalescent in front of it. From the medullary folds and the groove between them the neurocœle, and subsequently the entire nervous system, are developed as in Craniata in general (see p. 92). The portion of the blastoderm destined to give rise to the embryo becomes to a slight extent folded off from the rest, which forms an ill-defined rounded mass or *yolk-sac* to be subsequently absorbed as development proceeds. The most important features in the later stages (*F*) are the negative ones of the absence of the external gills (to be referred to subsequently in the account of the Amphibia) and the absence of horny jaws.

2. Distinctive Characters and Classification.

The Dipnoi are Pisces in which the notochord is persistent, and the primary cranium persists with little ossification, but has added to it a number of membrane-bones. The skull is autostylic, the lower jaw articulating with a palato-quadrate process which is immovably fixed to the side of the skull. There are four or five cartilaginous branchial arches. The dermal fin-rays are horny in character and are supported by numerous cartilaginous pterygiophores. The caudal fin is diphycercal. The paired fins are of the character of archipterygia. The pectoral arch is a single cartilage with a pair of superficial membrane-bones. The pelvic arch is well-developed and cartilaginous. There are gills attached to the branchial arches, and in addition a single or double lung opening into the pharynx. The gills are covered over by an operculum. There is a dermal skeleton in the form of overlapping cycloid

scales. There is a distinct cloaca. The intestine contains a spiral valve. The sinus venosus and the auricle are both imperfectly divided into two parts. There is a contractile conus arteriosus, which has a spirally twisted form, and is partly or completely divided internally by a longitudinal septum. The afferent branchial vessels take their origin close together immediately in front of the conus. A pulmonary artery is given off from the afferent branchial system; a pulmonary vein opens into the left-hand division of the sinus venosus. The optic nerves form a chiasma. The oviducts open anteriorly into the cœlome. The ova are of moderate size; segmentation is entire. So far as is known there is no metamorphosis.

The Dipnoi are classified as follows:—

Order 1.—Monopneumona.

Dipnoi in which the lung is single and the lateral jointed rays of the archipterygium are well developed.

This order comprises only the Australian *Ceratodus*.

Order 2.—Dipneumona.

Dipnoi in which the lung is double and the lateral rays of the archipterygium are vestigial or absent.

This order includes *Protopterus* (Fig. 863) of South Africa and *Lepidosiren* of South America.

3. General Remarks.

The three genera of living Dipnoi are closely allied in all the most essential features of their structure, and it will only be necessary now to mention the principal points in which Protopterus and Lepidosiren differ from Ceratodus. Of these, Protopterus is the better known, but the relationship between them is obviously so close that it is unlikely that there are any important differences with regard to the points that fall to be mentioned.

The limbs (Fig. 863) are long and very narrow, and the limb-skeleton is correspondingly modified, consisting of a slender, jointed axis without, or with only vestiges of, the lateral rows of rays. A blind dorsal diverticulum of the cloaca is present and perhaps corresponds to the rectal gland of the Elasmobranchs. There are two lungs, the anterior portions of which are united to form a median chamber, to which the presence of numerous trabeculæ gives a spongy character. There are five branchial arches, of which the last three bear the internal gills; in addition there is a series of external gills. The conus arteriosus is completely divided by a longitudinal septum. The pulmonary artery is given off from

the point of union of the efferent branchial arteries into a single lateral trunk. There is a single abdominal pore opening on the dorsal wall of the cloaca; this leads into a cavity into which the true abdominal pores, which are very minute, lead. The cerebral hemispheres are completely separated, except posteriorly, and the dorsal part of the mid-brain is not divided into optic lobes. The kidney (mesonephros) is elongated; it is devoid of nephrostomes in the adult state. The vasa deferentia, developed independently of the urinary system, join the unpaired terminal part of the Müllerian duct, which opens into the cloaca on a genital papilla.

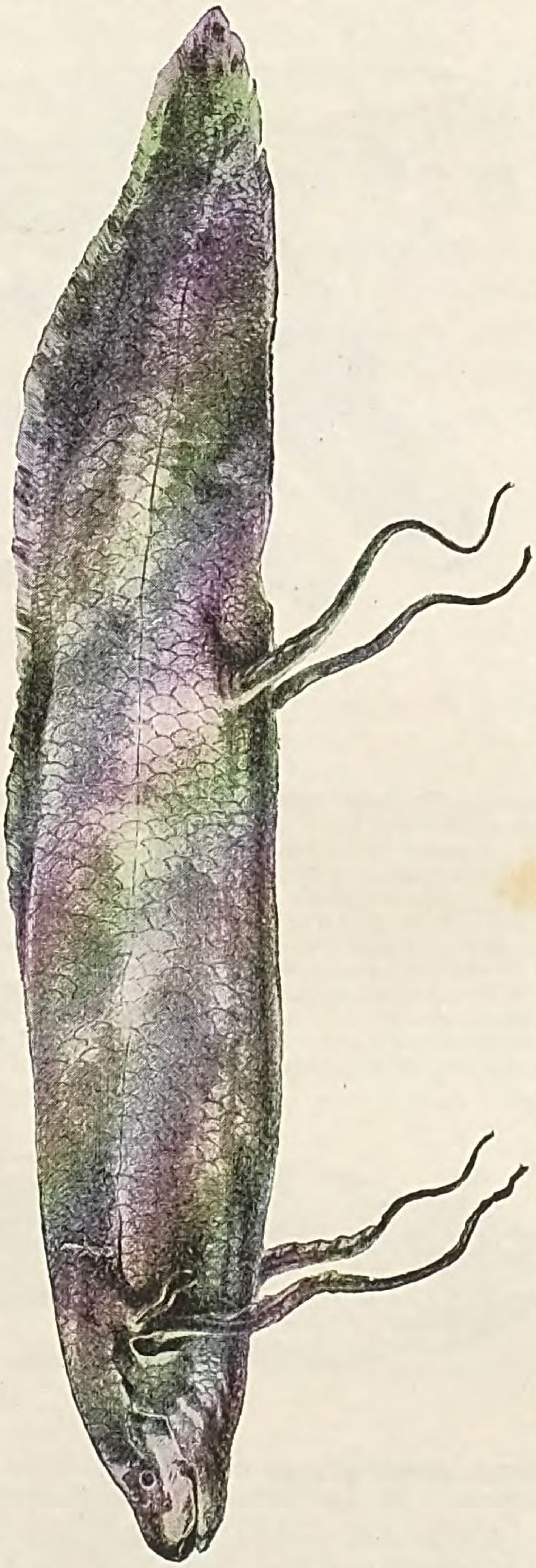


Fig. 863.—**Protopterus annectens.** Half the natural size. (After Dean.)

In accordance with these differences, and others of less importance, the living members of the class Dipnoi are divided into two orders—the *Monopneumona*, or one-lunged, and the *Dipneumona*, or two-lunged forms—the former comprising only Ceratodus, the latter Protopterus and Lepidosiren.

The Dipnoi are a very ancient race. The genus Ceratodus itself extends back to the early Mesozoic, and the remains of allied forms (*Dipterus* and other genera) are found in Devonian and Carboniferous formations. But if, as is conjectured, the *Arthrodira* are to be regarded as Dipnoi, then the group dates back as far as the Silurian. The evidence for this conclusion is, however, by no means complete, as our knowledge of the structure of the extinct Fishes in question is necessarily meagre. They had the head and anterior part of both dorsal and ventral surfaces (Fig. 865) protected by bony plates, the system of head-plates being connected with those

on the back by a well-developed movable joint. The notochord was persistent, and the cranium apparently cartilaginous ; the mandible was autostylic. There were composite cutting dental plates. The

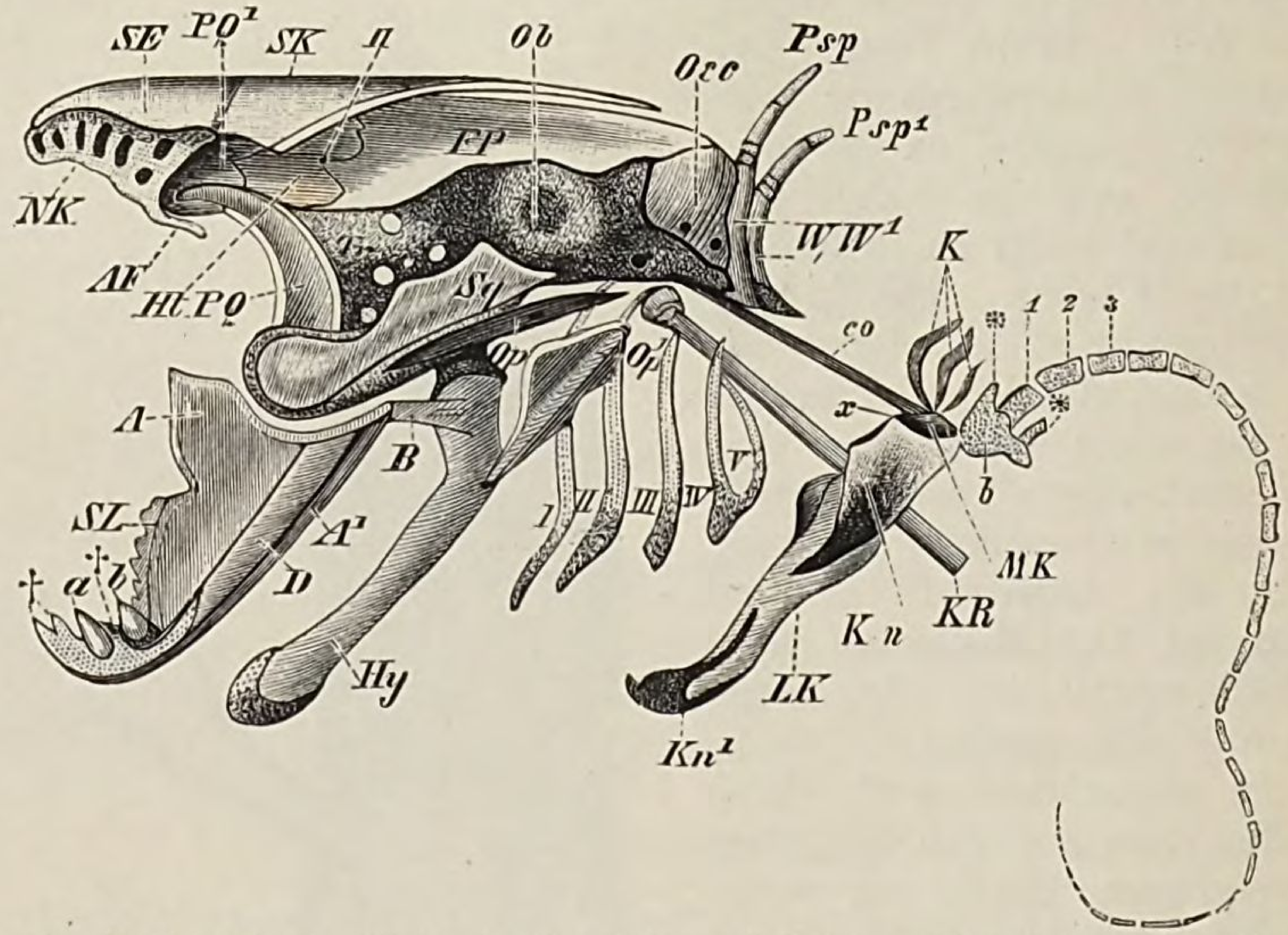


FIG. 864.—**Protopterus.** Skull, shoulder-girdle, and skeleton of fore-limb. *AA*, articular bone of lower jaw : *AF*, præ-orbital process ; *a* and *b* (on lower jaw), teeth ; *b*, basal cartilage of pectoral fin ; *B*, ligamentous band connecting the mandible with the hyoid ; *co*. ligamentous band connecting the dorsal end of the pectoral arch with the skull ; *D*, dentary of mandible ; *FP*, fronto-parietal ; *Ht*, membranous fenestra perforated by the foramen for the optic nerve (II) ; *Hy*. hyoid ; *Kn*,*Kn'*, cartilage of the pectoral arch ; *KR*, occipital rib ; *LK* and *MK*, investing bones of the pectoral arch ; *NK*, olfactory capsule ; *Ob*, auditory capsule ; *Occ*. supra-occipital ; *Op*. and *Op'*. rudimentary opercular bones ; *PQ*. palato-quadrate ; *Psp*. *Psp'*. spinous processes of the anterior vertebræ ; *SE*. supra-ethmoid bone ; *SK*, roofing membrane-bones ; *SL*, enamel ridge of tooth ; *Tr*. trabecula with the openings for the trigeminal and facial nerves ; *WW'*, anterior vertebræ coalescent with the skull ; 1, 2, 3, segments of axis of pectoral fin ; *,*, rudimentary lateral rays of pectoral fin. (From Wiedersheim.)

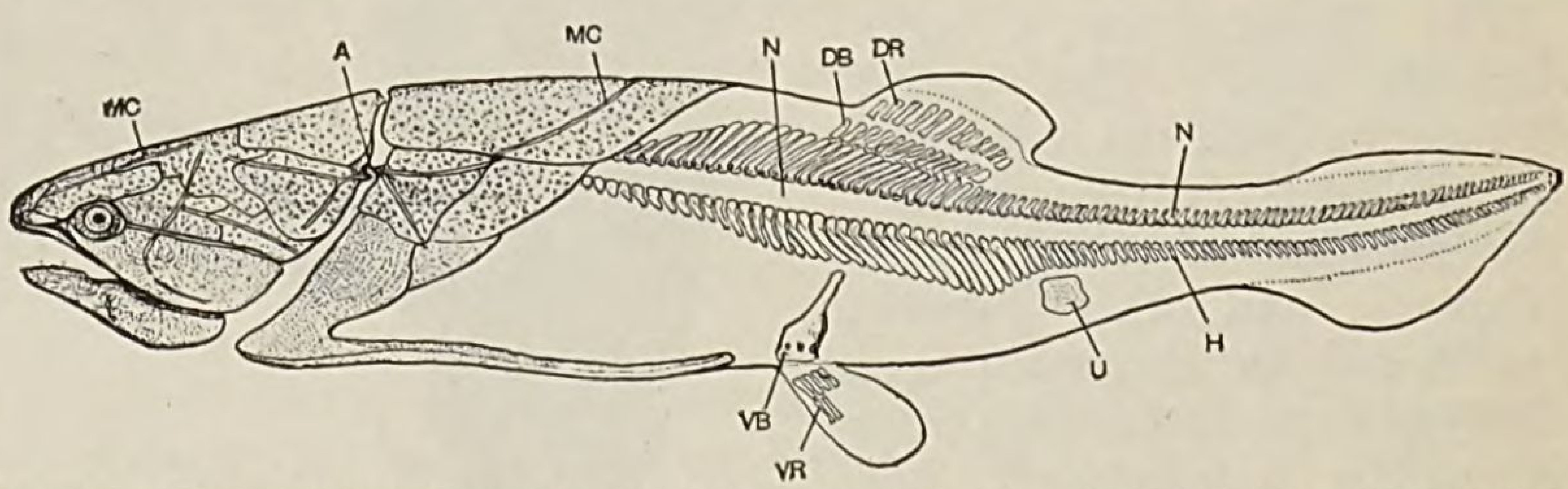


FIG. 865.—**Coccosteus decipiens**. Side view, restored. *A*, articulation of head with trunk. *DB*, cartilaginous basals of dorsal fin. *DR*, cartilaginous radials of dorsal fin. *H*, hæmal arch and spine. *MC*, mucous canals. *N*, neural arch and spine. *U*, median unpaired plate of hinder ventral region. *VB*, basals of pelvic fin. *VR*, radials of pelvic fin. (From Dean, after Smith Woodward.)

pectoral fins are unknown ; the rays of the small pelvic (*VR*) were supported on a flattened plate (*VB*).

With some special features of their own the Dipnoi combine characteristics in which they resemble now one, now another, of

the other groups of Fishes, together with a few in which they approach the next class of Vertebrates to be dealt with, viz. the Amphibia. The brain and the heart are quite peculiar: the former in its undivided, or almost undivided, mid-brain; the latter in its imperfectly divided sinus and auricle, and spirally twisted conus. In the limbs the Dipnoi are only closely approached by certain extinct Elasmobranchs (p. 155). In the presence of a cloaca and a spiral valve they also approach that sub-class, as well as in the contractile conus—the two last features being also shared with the Ganoid Teleostomi. The operculum with its supporting bones connects them with the Teleostomi. The Amphibian features will be best referred to at a later stage. On the whole, though in some respects more primitive than the members of the other sub-classes of Pisces, the Dipnoi tend to establish a connection between that class and the Amphibia.

APPENDIX TO PISCES.

THE OSTRACODERMI

The Ostracodermi are a group of Palæozoic Fishes of uncertain affinity, characterised by the extraordinary development of the exoskeleton of the head and trunk, and the absence, in all the fossil remains hitherto found, of endo-skeleton, including jaws. It may therefore be assumed that there was a persistent notochord, and that the rest of the skeleton was unossified. It is uncertain whether the group should be considered the equivalent of a Class or of a Sub-class: it is divisible into three orders, which are best considered separately.

Order 1.—Heterostraci.

This order includes a single family of three genera: *Pteraspis* may be taken as an example (Fig. 866). The body is elongated, and divided into an anterior region,

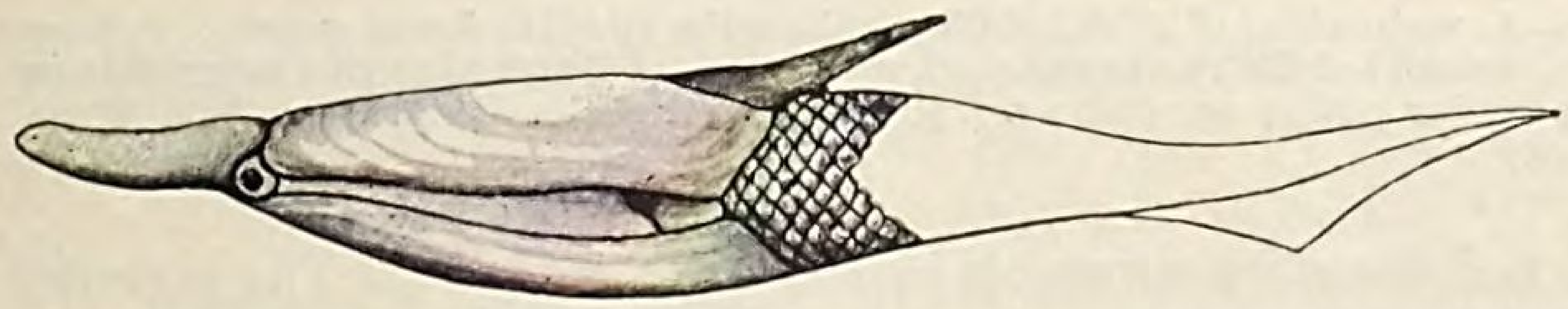


Fig. 866.—**Pteraspis rostrata** (Devonian). (From the Brit. Mus. Cat. of Fossil Fishes.)

representing the head and fore-part of the trunk, and covered by strong calcified plates or scutes, and a posterior or caudal region covered by rhomboidal scales. In the anterior region there are seven scutes above, constituting the *dorsal shield*, while below there is a single *ventral shield*. The dorsal shield is produced into a rostrum, and is hollowed by a pair of lateral orbits, between which is a pit, on the inner surface of the shield, probably marking the position of the pineal body. The scutes contain no lacunæ or canaliculi, and have not, therefore, the structure of bone: they are lined by a nacreous layer, and are covered externally with a layer of vaso-dentine. The tail appears to have been heterocercal, but there is no trace of paired fins.

ORDER 2.—OSTEOSTRACI.

Cephalaspis (Fig. 867) may be taken as an example of the five genera included in this order. The head is covered with a calcified shield, which has a curious resemblance to the cephalic shield of Limulus or of a Trilobite, being gently curved above, produced behind into spines, continued ventrally into a sub-frontal plate (B, *s. f. p.*), and having a pair of orbits (A, *or*) for the eyes near the middle of the dorsal surface. Behind the shield, towards the ventral surface, is a plate which probably supported the operculum (C, *op.*). The scutes contain some

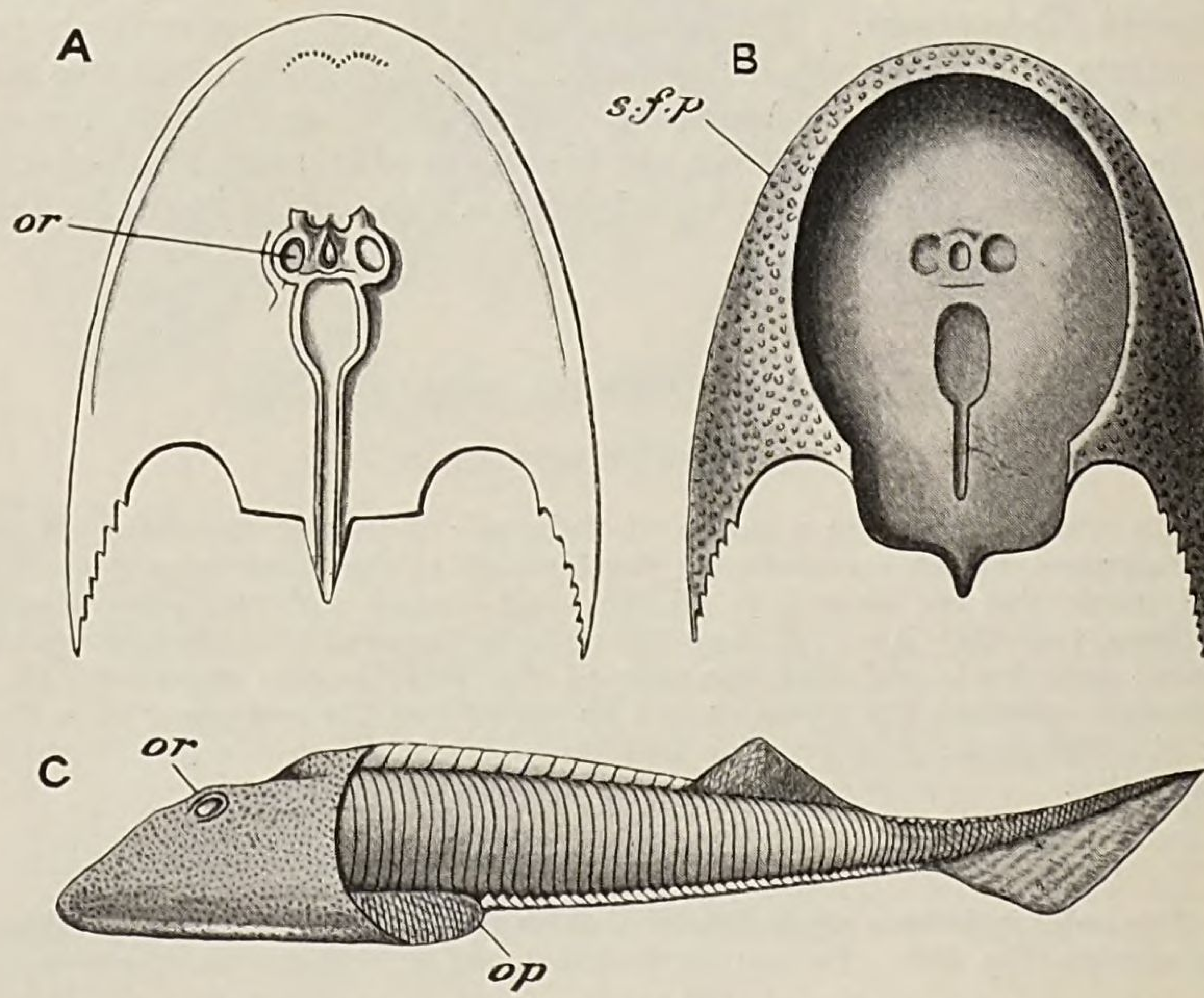


FIG. 867.—A, restoration of shield of **Cephalaspis lyelli,** dorsal aspect; B, diagram of ventral aspect of shield of **Cephalaspis;** C, restoration of **Cephalaspis murchisoni** (Devonian). *op.* opercular plate; *or.* orbit; *s. f. p.* sub-frontal plate. (From the Brit. Mus. Cat. of Fossil Fishes.)

lacunæ, and therefore approach in structure to bone. The posterior portion of the body is covered by deep, narrow scales; there is a single dorsal and a heterocercal tail fin, but no trace of paired fins is known.

ORDER 3.—ANTIARCHA.

This group contains five genera, of which *Pterichthys* (Fig. 868) may be taken as an example. It presents a broad and high anterior region, covered by articulated plates which have the structure of bone and are covered by a layer of enamel, and a caudal region covered by rounded or hexagonal scales. The orbits are placed close together on the top of the head, and between them is a plate pitted on its inner surface, apparently for the pineal body. There is a pair of large pectoral fins (*pct. f.*) covered by strong scutes, a single dorsal fin (*d. f.*) with fulcra but apparently no fin-rays, and a heterocercal tail-fin (*c. f.*).

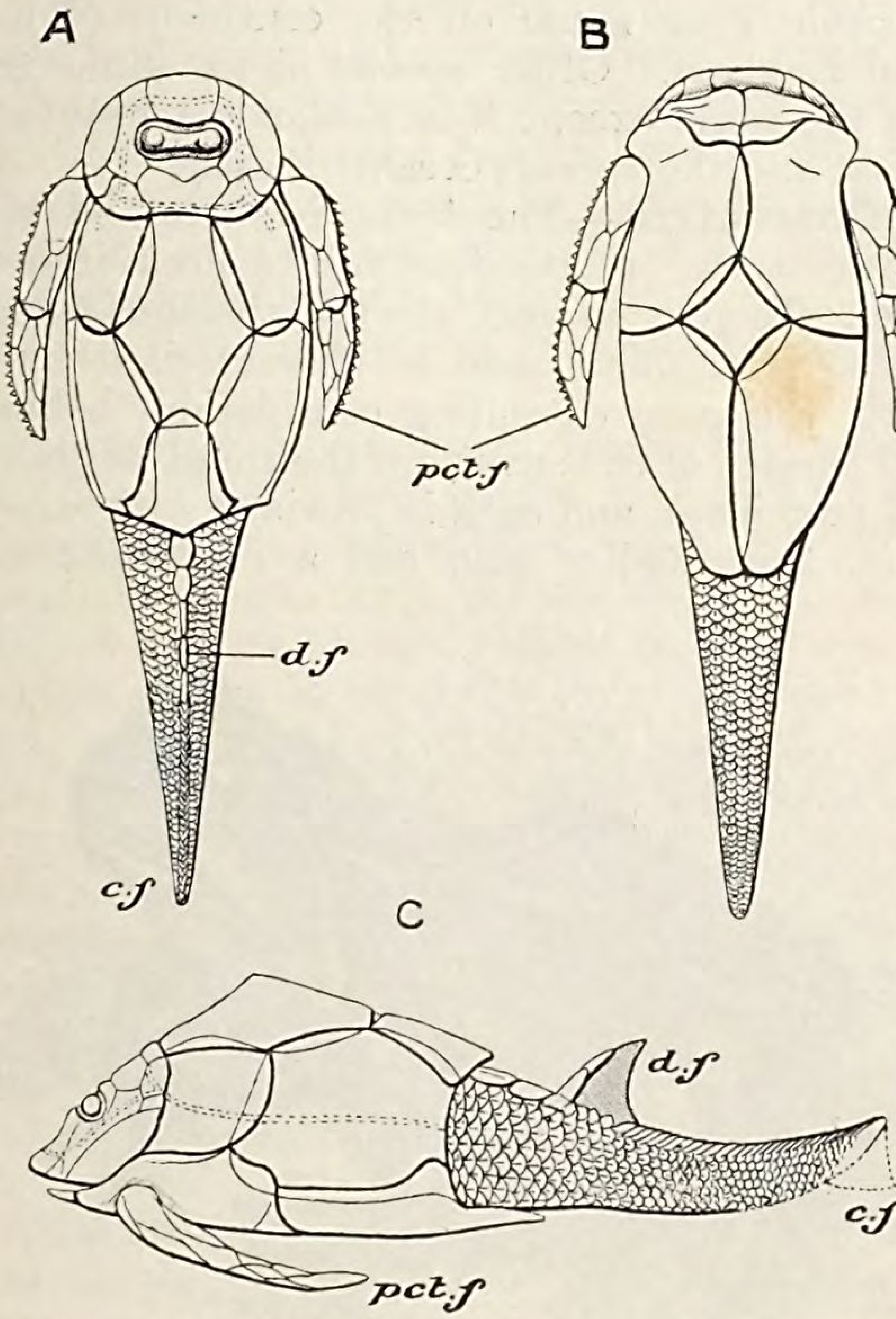


FIG. 868.—**Pterichthys testudinarius.** A, dorsal; B, ventral; C, lateral aspect. *c. f.* caudal fin; *d. f.* dorsal fin; *pct. f.* pectoral fin. (From the Brit. Mus. Cat. of Fossil Fishes.)

CLASS IV.—AMPHIBIA.

The Amphibia are distinguished from Fishes by the possession of pentadactyle limbs instead of paired fins, and by the absence of fin-rays in the median fins. They nearly all breathe by gills in the larval condition, and many of them retain those organs throughout life; lungs are, however, usually present in the adult. The class includes the Frogs, Toads, Newts, and Salamanders, as well as the peculiar snake-like Cæcilians, and the gigantic extinct Stegocephala or Labyrinthodonts.

1. EXAMPLE OF THE CLASS.—THE COMMON FROG (*Rana temporaria*), OR THE EDIBLE FROG (*Rana esculenta*).

Rana temporaria is the common British species of Frog, found in ponds and damp situations all over the country; *R. esculenta* is the

large green edible Frog found on the continent of Europe and occasionally in England. Other species of the same genus occur in all parts of the world except New Zealand, the southern part of South America, and the various oceanic islands.

External Characters.—The *trunk* is short and stout, and is continued, without the intermediation of a neck, into the broad, depressed *head*. There is no trace of a tail, the anus being terminal. The *mouth* also is terminal, and is characterised by its extraordinary width, the gape extending considerably behind the eye. On the dorsal surface of the snout are the small *nostrils*; the *eyes* are large and prominent, and each is provided with an *upper eyelid* in the form of a thick fold of skin and a *nictitating membrane*, a



FIG. 869.—**Rana temporaria.** (From Mivart.)

much thinner fold, which arises from the lower margin of the eye and can be drawn up over it. Close behind the eye is a circular area of tensely-stretched skin, the *tympanic membrane*, a structure not met with in any Fish: as we shall see, it is an accessory auditory organ. There is no trace of branchial apertures.

The back has a peculiar bend or hump, in the sitting posture, marking the position of the sacral vertebra. The limbs are of very unequal size. The *fore-limbs* are short, and each consists of an *upper arm*, which, in the ordinary position, is directed backwards and downwards from the shoulder-joint; a *fore-arm*, directed downwards and forwards from the elbow; and a *hand*, ending in four short tapering *digits*, directed forwards. The *hind-limb* is of great size; in the usual squatting posture the *thigh* is directed

downwards, outwards, and forwards from the thigh-joint, the *shank* inwards, backwards, and upwards from the knee. The *foot* consists of two parts, a *tarsal region* directed downwards from the heel-joint, and five long, slender *digits* united by thin folds of skin or *webs.* Thus the limbs are placed in such a way that the elbow and knee face one another, and the first digit, that of the hand probably representing the *index-finger*, that of the foot, the *hallux* or great toe, is turned inwards or towards the median plane of the body.

The *skin* is greyish-brown in R. temporaria, greenish in R. esculenta, and is mottled, in both species, with dark brown or black; in R. temporaria there is a large black patch over the tympanic region. Sexual differences occur in both species; in R. temporaria there is a large, black, glandular swelling on the inner side of the hand of the male, and in R. esculenta the male has, at each angle of the mouth, a loose fold of skin, the *vocal sac,* which can be inflated from the mouth into a globular form. The skin is soft and slimy owing to the secretion of mucous glands; there is no trace of exoskeleton.

Endo-skeleton.—The *vertebral column* (Fig. 870) is remarkable for its extreme shortness; it consists of only nine vertebræ (V.1—V.9), the last followed by a slender, bony rod, the *urostyle* (U. ST). The second to the seventh vertebræ have similar characters. The *centrum* (B, *cn*) is somewhat depressed and has a concave anterior and a convex posterior face, a form known as *procœlous.* Each half of the *neural arch* consists of two parts, a pillar-like *pedicle* (*pd*) springing from the centrum and extending vertically upwards, and a flat, nearly horizontal *lamina* (*lm*), forming, with its fellow, the roof of the neural canal. When the vertebræ are in position wide gaps are left between successive pedicles; these are the *inter-vertebral foramina* and serve for the transmission of the spinal nerves. The *zygapophyses* (*a. zyg*) or yoking processes are far better developed than in any Fish; they spring from the junction of pedicle and lamina, the anterior zygapophysis having a distinct articular facet on its dorsal, the posterior on its ventral surface. Thus when the vertebræ are in position the posterior zygapophyses of each overlap the anterior zygapophyses of its immediate successor. Laterally the neural arch gives off on each side a large outstanding *transverse process* (*tr. pr*); its crown is produced into a very small and inconspicuous *neural spine* (*n. sp*).

The first or *cervical vertebra* (V.1) has a very small centrum and no transverse processes. There are no anterior zygapophyses, but at the junction of centrum and arch there occurs on each side a large oval concave facet for articulation with one of the condyles of the skull (*vide infra*). The eighth vertebra has a biconcave centrum; that of the ninth or *sacral vertebra* (V.9) is convex in

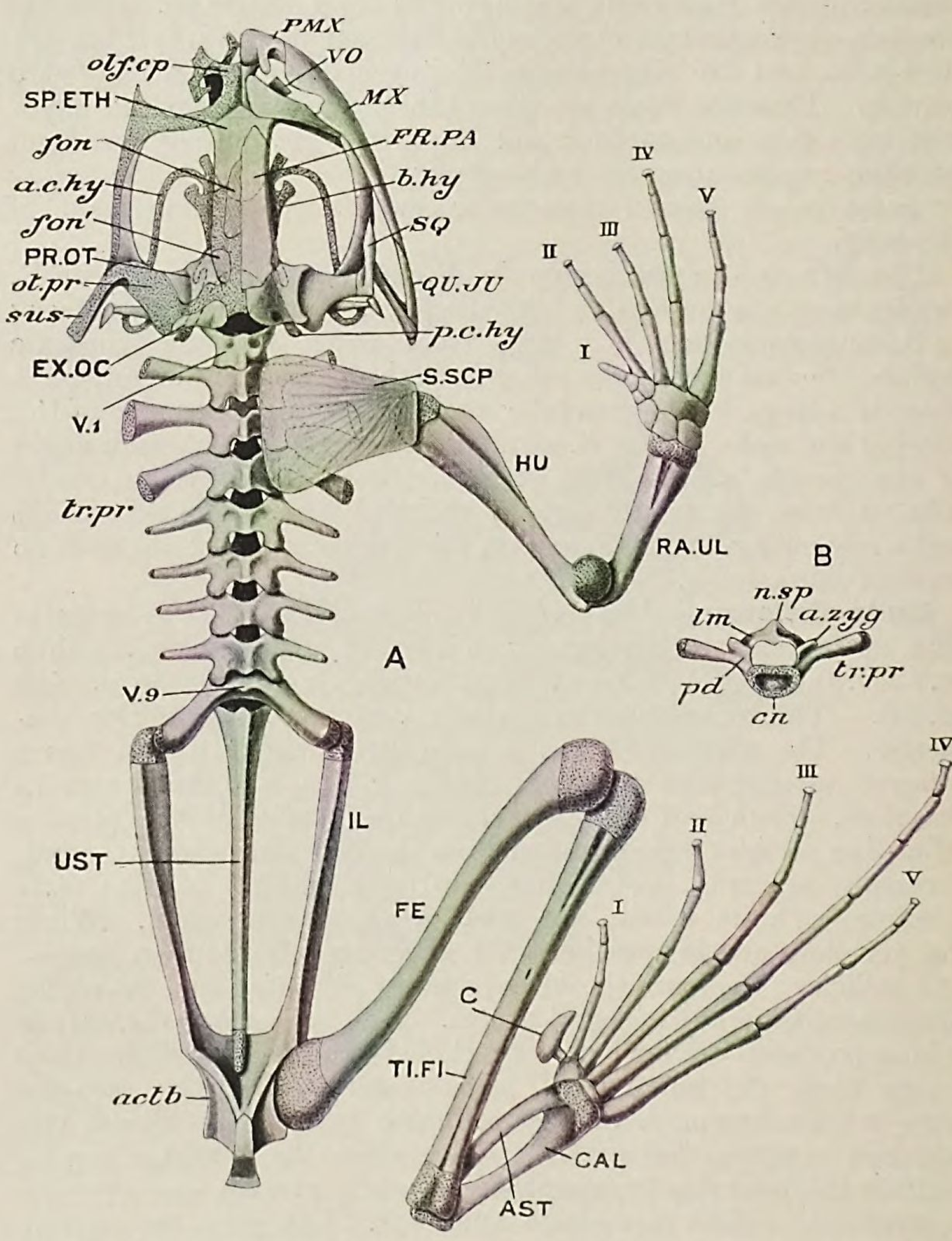


FIG. 870.—**Rana temporaria.** A, the skeleton from the dorsal aspect; the left half of the shoulder girdle and the left fore and hind limbs are removed, as also are the membrane bones on the left side of the skull. Cartilaginous parts dotted. Names of cartilage bones in thick, those of membrane bones in italic capitals. *a. c. hy.* anterior cornu of hyoid; *actb.* acetabulum; **AST.** astragalus; *b. hy.* basi-hyal; **C.** calcar; **CAL.** calcaneum; **EX. OC.** ex-occipital; **FE.** femur; *fon. fon.'* fontanelles; *FR. PA.* fronto-parietal; **HU.** humerus; **IL.** ilium; *MX.* maxilla; *olf. cp.* olfactory capsule; *ot. pr.* otic process; *p. c. hy.* posterior cornu of hyoid; *PMX.* premaxilla; **PR.OT.** pro-otic; **RA.UL.** radio-ulna; **SP.ETH.** sphen-ethmoid; *SQ.* squamosal; **S.SCP.** supra-scapula; *sus.* suspensorium; **TI.FI.** tibio-fibula; *tr. pr.* transverse process; **U.ST.** urostyle; **V. 1,** cervical vertebra; **V.9,** sacral vertebra; *VO.* vomer; *I—V*, digits. B, the fourth vertebra, anterior face. *a. zyg.* anterior zygapophysis; *cn.* centrum; *lm.* lamina; *n. sp.* neural spine; *pd.* pedicle; *tr. pr.* transverse process. (After Howes, slightly altered.)

front and presents posteriorly a double convexity articulating with a double concavity on the anterior end of the urostyle. The latter (U. ST) is formed by the ossification of the perichordal tube (see p. 67) which, in this region of the vertebral column, does not become segmented into vertebræ.

The *skull* (Figs. 870 and 871) consists of a narrow *brain-case*, produced behind into great outstanding *auditory capsules*, and in front into large *olfactory capsules*. The whole of the bones of the *upper jaw* are immovably fixed to the cranium so that the only free parts are the *lower jaw* and a small plate of mingled bone and cartilage, the *hyoid apparatus*, which supports the tongue and is the sole representative of the entire visceral or gill-bearing skeleton of Fishes.

As in the Trout, a number of membrane bones can be removed from the skull without injury to the underlying chondrocranium. The latter, however, is not, as in the Trout, the primary cranium alone, but, as in Holocephali and Dipnoi, the primary cranium *plus* the palato-quadrate or primary upper jaw. The cranium in the strict sense includes the brain-case and the auditory and olfactory capsules: the palato-quadrate (*pal. qu*) is not a solid mass fused throughout its length with the cranium, as in Holocephali and Dipnoi, but rather resembles the subocular arch of the Lamprey (p. 118), being a slender rod attached to the cranium at either end, but free in the middle. It is divisible into three regions, a posterior *quadrate region* or *suspensorium* (Fig. 870, *sus*), an intermediate *pterygoid region*, and an anterior *palatine region*. The suspensorium extends backwards, outwards, and downwards from the auditory region of the cranium, to which it is immovably united by its forked proximal end, one branch of the fork—the *otic process* (Fig. 871, *ot. pr*)—being fused with the auditory capsule, the other—the *pedicle* (*ped*)—with the trabecular region immediately anterior to the auditory capsule. Ventrally the suspensorium furnishes an articular facet for the mandible and is connected with the delicate rod-like pterygoid region; this passes forwards and joins the palatine region, which is a transverse bar fused at its inner end with the olfactory capsule.

The occipital region of the cranium contains only two bones, the *exoccipitals* (EX. OC), which lie one on each side of the foramen magnum (*for. mag*) and meet above and below it: there is no trace of supra- or basi-occipital. Below the foramen magnum are paired oval projections, the *occipital condyles* (*oc. cn*), furnished by the exoccipitals and articulating with the cervical vertebra.

Each auditory capsule is ossified by a single bone, the *pro-otic* (PR. OT); the remaining ossifications of the auditory region (p. 72) are not developed. In the adult the pro-otic fuses with the exoccipital: it presents on its outer surface, behind the otic process of the suspensorium, a small aperture, the *fenestra ovalis*, closed in the entire animal by membrane, and, when the latter is removed,

leading into the cavity of the auditory capsule containing the membranous labyrinth.

In front of the auditory capsules a considerable part of the cranial wall is formed of cartilage, and presents above a single large and a pair of small *fontanelles* (Fig. 870, *fon. fon'*) but anteriorly it is ossified by the *sphen-ethmoid*, or *girdle-bone* (SP. ETH), a short bony tube divided by a transverse partition into an anterior compartment which lodges the hinder ends of the olfactory sacs, and a posterior compartment which contains the olfactory lobes. The anterior compartment is again divided by a vertical partition which separates the olfactory sacs from one

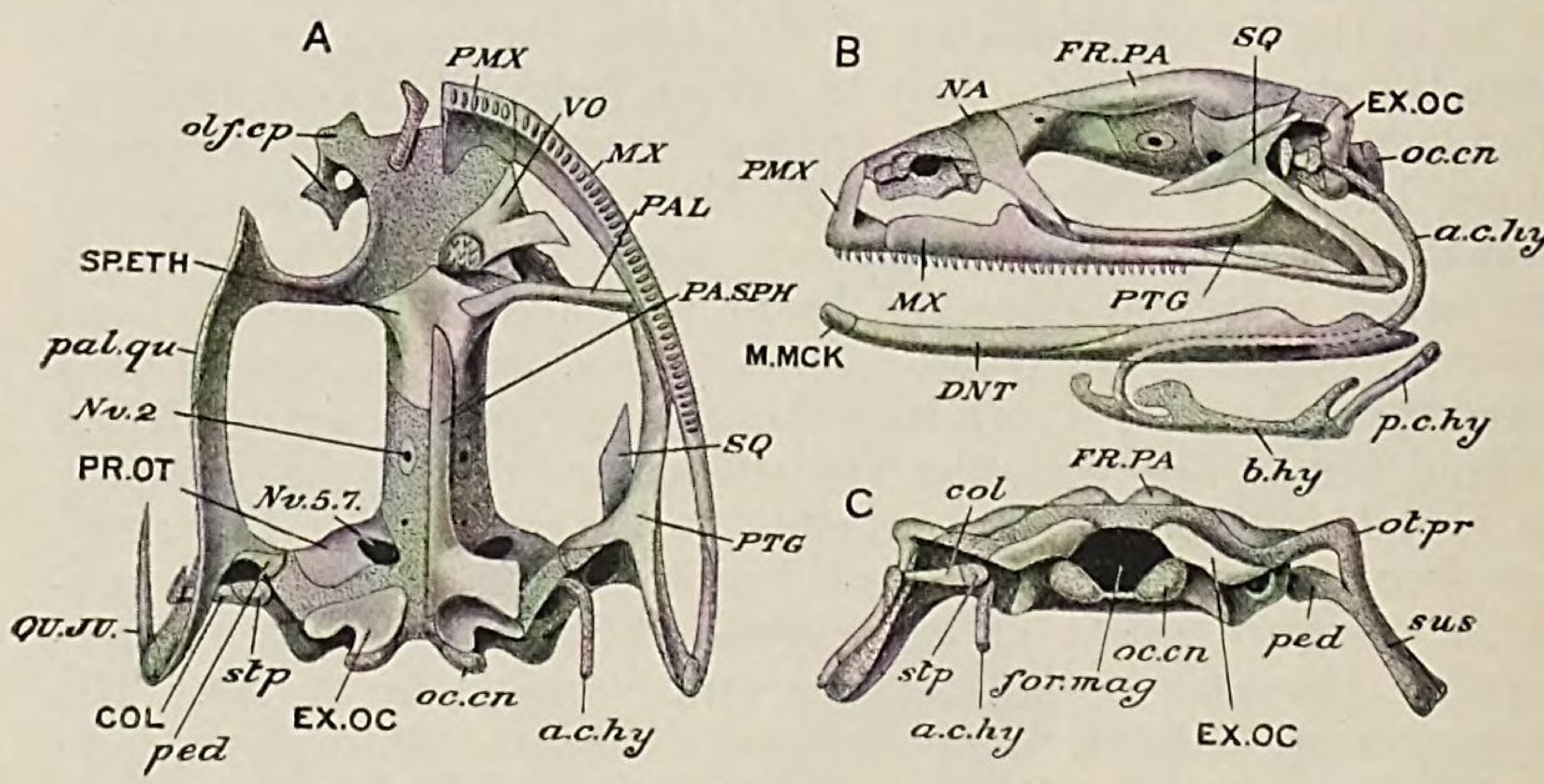


FIG. 871.—**Rana temporaria.** The skull. A, from beneath, with the membrane bones removed on the right side (left of figure); B, from the left side, with mandible and hyoid; C, from behind. *a. c. hy.* anterior cornu of hyoid; *b. hy.* body of hyoid; **COL.** columella; *DNT.* dentary; **EX.OC.** ex-occipital; *for. mag.* foramen magnum; *FR. PA.* fronto-parietal; **M.MCK.** mento-meckelian; *MX.* maxilla; *NA.* nasal; *Nv. 2*, optic foramen; *Nv. 5, 7*, foramen for fifth and seventh nerves; *oc. cn.* occipital condyle; *olf. cp.* olfactory capsule; *ot. pr.* otic process; *PAL.* palatine; *pal. qu.* palato-quadrate; *PA.SPH.* parasphenoid; *p. c. hy.* posterior cornu of hyoid; *ped.* pedicle; *PMX.* premaxilla; **PR.OT.** pro-otic; *PTG.* pterygoid; *QU.JU.* quadrato-jugal; **SP.ETH.** sphenethmoid; *SQ.* squamosal; *stp.* stapes; *VO.* vomer. (After Howes, slightly altered.)

another, and the transverse partition is perforated for the olfactory nerves. This very peculiar and characteristic bone may be taken to represent meso- and ecto-ethmoids and pre- and orbitosphenoids all united together.

The olfactory capsules (*olf. cp*) have a delicate cartilaginous roof and floor produced into irregular processes which help to support the olfactory sac. They are separated from one another by a vertical plate of cartilage, continuous behind with the girdle-bone and representing the unossified part of the mesethmoid, and the anterior wall of each is produced into a little curved, rod-like *rhinal process.* The whole of the palato-quadrate arch is unossified.

To this partly ossified chondrocranium the usual membrane

bones are applied above and below. Covering the roof of the brain-case is a single pair of bones, the *fronto-parietals* (*FR. PA*), each formed by the fusion of a frontal and a parietal, distinct in the young Frog. Over the olfactory capsules are paired triangular *nasals* (*NA*), and applied to their ventral surfaces small paired *vomers* (*VO*). On the ventral surface of the skull is a large T-shaped *parasphenoid* (*PA. SPH*), its stem underlying the basis cranii, while its two arms extend outwards beneath the auditory capsules.

In the Trout, it will be remembered, the palatine and pterygoid are cartilage bones, formed as ossifications of the palato-quadrate cartilage. In the Frog this cartilage is, as we have seen, unossified, but to its ventral face two membrane bones are applied, a small rod-like *palatine* (*PAL*), and a three-rayed *pterygoid* (*PTG*) having an anterior arm extending forwards to the palatine, an inner arm applied to the pedicle of the suspensorium, and an outer arm extending along the whole inner face of the suspensorium. It will be seen that, as we ascend the animal series, bones originally preformed in cartilage may give place to membrane bones, developed in corresponding situations, but altogether independent of the cartilage, the latter remaining unossified.

The suspensorium, as we have seen, is strengthened on its inner face by the outer arm of the pterygoid; externally it is similarly supported by a hammer-shaped membrane bone, the *squamosal* (*SQ*). The upper jaw is formed by three membrane bones, the small *premaxilla* (*PMX*) in front, then the long, narrow *maxilla* (*MX*), and finally the short *quadrato-jugal* (*QU. JU*), which is connected posteriorly with the quadrate.

The mandible contains a persistent *Meckel's cartilage*, as a sort of core, outside which are formed two membrane-bones, a long *angulo-splenial* on its inner face, and a short *dentary* (*DNT*) on the outer face of its distal half. The actual distal end of Meckel's cartilage is ossified as a small cartilage bone not represented in Fishes, the *mento-meckelian* (M. MCK).

The *hyoid apparatus* consists of a shield-shaped plate of cartilage, the *body of the hyoid* (*b. hy*), produced at its anterior angles into slender rods, the *anterior cornua* (*a. c. hy*), which curve upwards and are fused with the auditory capsules, and at its posterior angles into partly ossified rods, the *posterior cornua* (*p. c. hy*), which extend backwards, embracing the glottis.

Two other cranial structures remain to be noticed. External to the squamosal is a ring of cartilage, the *annulus tympanicus* (Fig. 882, *an. tymp.*), which supports the tympanic membrane as the frame of a tambourine supports the parchment. Inserted into the fenestra ovalis is a nodule of cartilage, the *stapes* (*stp*), to which is attached the inner end of a small hammer-shaped structure, the *columella* (COL), the handle of which is ossified, while its

cartilaginous head, or *extra-columella*, is fixed to the inner surface of the tympanic membrane.

The comparison of the Frog's skull with those of Fishes is facilitated by a study of its development. In the Tadpole or larval Frog there is a cartilaginous cranium (Fig. 872) connected on each side with a stout inverted arch, like the subocular arch of the Lamprey or the palato-quadrate of Chimæra or Ceratodus, and, like them, developed from the dorsal region of the mandibular arch. The quadrate region (*qu*) of this primary upper jaw is well in front of the eye, the axis of the suspensorium being inclined forwards and the mandible very short, in correspondence with the small size of the Tadpole's mouth. The quadrate is fused by its pedicle with the trabecular region, the otic process (*ot. pr*) which unites it with the auditory capsule being formed later. Behind the suspensorium are distinct hyoid (*c. hy*) and branchial (*br. 1–4*) arches supporting the gills by which the tadpole breathes. As development goes on, the axis of the suspensorium is rotated backwards, producing the wide gape of the adult, and the stout palatopterygoid region of the subocular arch (*pal. ptg*) gradually assumes the slender proportions it has in the adult. The greater part of the hyoid arch gives rise to the anterior cornua of the adult hyoid apparatus, the body of which is formed from the basihyal and basi-branchials, and its posterior cornua probably from the fourth branchial arch. The columella is developed independently, but may perhaps represent a pharyngo-hyal or dorsal segment of the hyoid arch. The stapes is a detached portion of the outer wall of the auditory capsule. Thus, with the assumption of purely aërial respiration, the complex branchial skeleton is reduced to a simple structure for the support of the tongue.

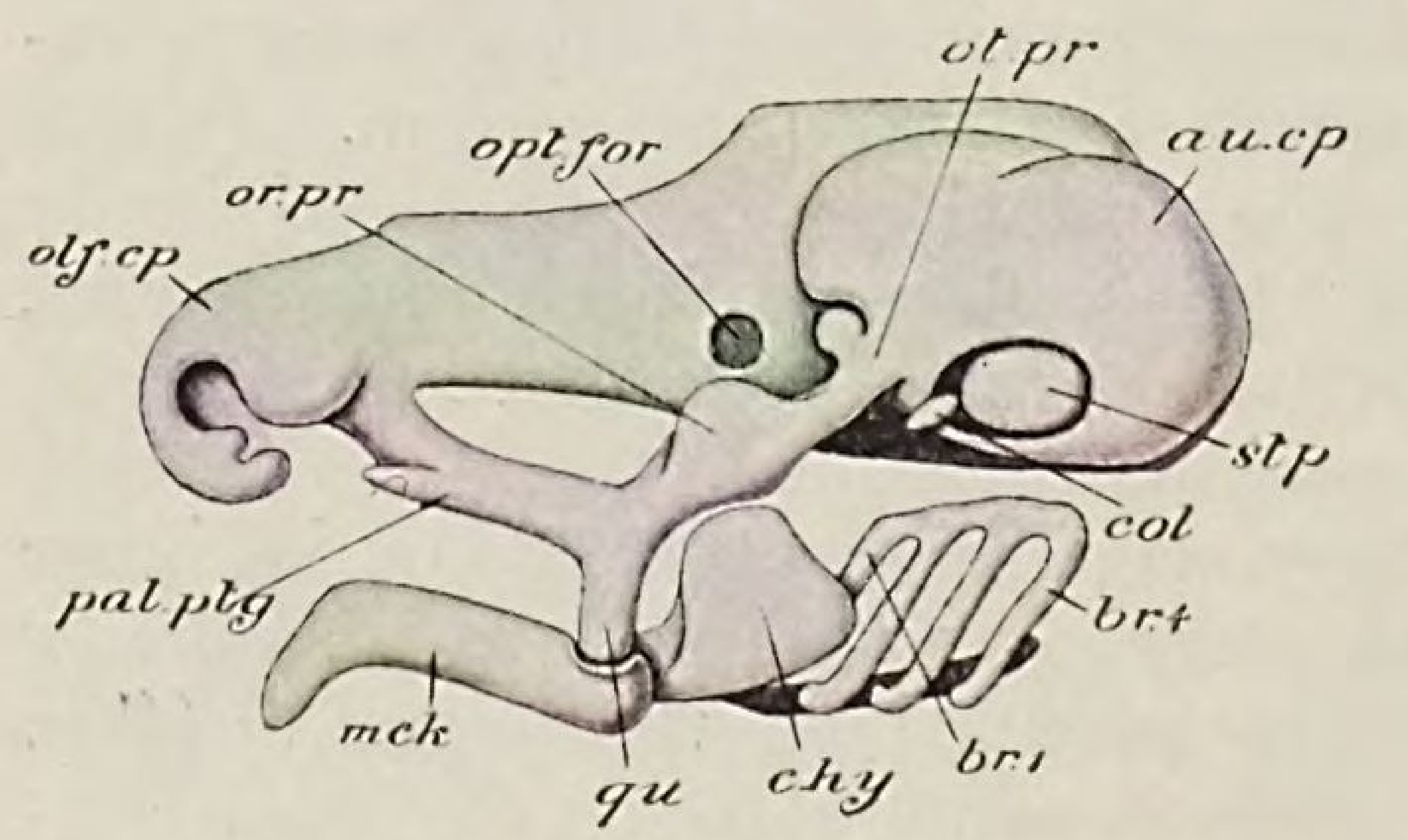


FIG. 872.—Skull of **Tadpole**. *au. cp.* auditory capsule; *br. 1—4*, branchial arches; *c. hy.* ceratohyal; *col.* columella; *mck.* Meckel's cartilage; *olf. cp.* olfactory capsule; *opt. for.* optic foramen; *or. pr.* orbital process of suspensorium; *ot. pr.* otic process; *pal. ptg.* palato-pterygoid bar; *qu.* quadrate; *stp.* stapes. (After Marshall, slightly altered.)

The *shoulder-girdle* has essentially the structure already described (p. 77) in general terms as characteristic of the pentadactyle Craniata. The *scapula* (Fig. 873, *S*) is ossified, and is connected by its dorsal edge with a *supra-scapula* (Fig. 870, S. SCP) formed partly of bone, partly of calcified cartilage, and developed from the dorsal region of the embryonic shoulder-girdle. The *coracoid* (*Co*) is also ossified, but the *procoracoid* is represented by

a bar of cartilage, having a membrane bone, the *clavicle* (*Cl*), closely applied to it. The supra-scapula overlaps the anterior vertebræ; the coracoid and procoracoid are connected ventrally by a cartilage, the *epicoracoid* (*Co'*) which is in close contact with its fellow of the opposite side in the middle ventral line, so that the entire shoulder-girdle, like that of the Dog-fish, forms a single inverted arch.

Passing forwards from the anterior ends of the united epicoracoids is a rod of bone, the *episternum* (*Ep.*), tipped by a rounded plate of cartilage, the *omosternum*; and passing backwards from their posterior ends is a similar but larger bony rod, the

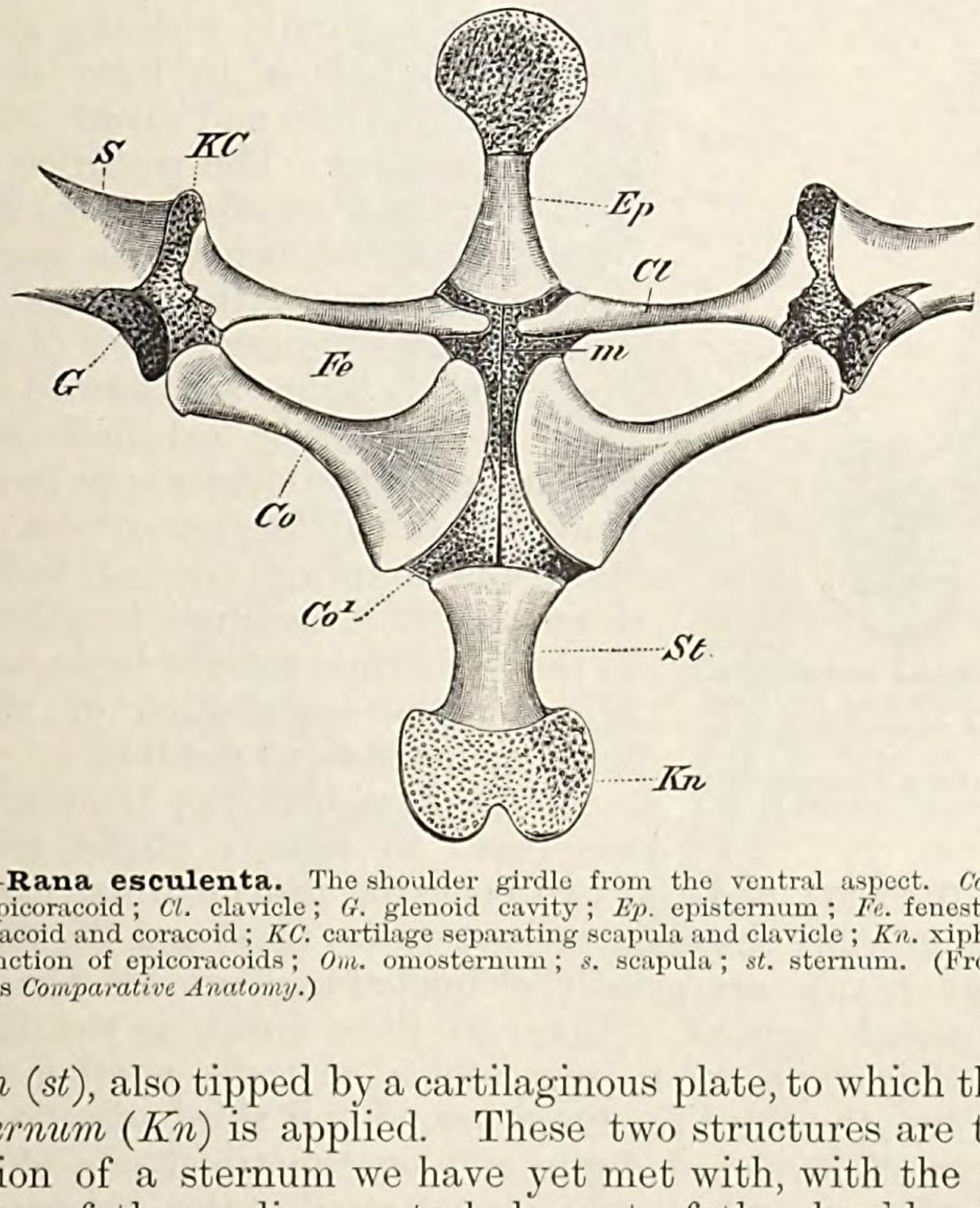


FIG. 873.—**Rana esculenta.** The shoulder girdle from the ventral aspect. *Co.* coracoid; *Co.'* epicoracoid; *Cl.* clavicle; *G.* glenoid cavity; *Ep.* episternum; *Fe.* fenestra between procoracoid and coracoid; *KC.* cartilage separating scapula and clavicle; *Kn.* xiphi-sternum; *m*, junction of epicoracoids; *Om.* omosternum; *s.* scapula; *st.* sternum. (From Wiedersheim's *Comparative Anatomy*.)

sternum (*st*), also tipped by a cartilaginous plate, to which the name *xiphisternum* (*Kn*) is applied. These two structures are the first indication of a sternum we have yet met with, with the possible exception of the median ventral element of the shoulder-girdle of Notidanus (p. 162). The omosternum is developed as paired forward extensions of the epicoracoids which undergo fusion: the sternum and xiphi-sternum arise as paired rods lying posterior to the epicoracoids, and subsequently uniting with one another.

The *fore-limbs* deviate from the typical structure (p. 76) chiefly in the fusion of the radius and ulna into a single *radio-ulna* (Fig. 870, RA. UL), and in the presence of only four complete digits with a vestigial one on the radial side. In all probability

the latter represents the pollex, and the complete digits are the second to the fifth of the typical hand. Six carpals only are present, the third, fourth, and fifth digits articulating with a single bone which has apparently arisen by the fusion of the third, fourth, and fifth distalia and of at least one centrale.

The *pelvic girdle* (Fig. 874) is very peculiarly modified; it resembles in form a Bird's "merrythought," consisting of two long curved bars articulating in front with the transverse processes of the sacral vertebra (Fig. 870) and uniting posteriorly in an irregular vertical disc of mingled bone and cartilage which bears on each side a deep, hemispherical *acetabulum* (*G*) for the articulation of the thigh-bone. The curved rods are the *ilia* (*Il.*, *P*); they expand posteriorly and unite with one another in the median plane to form the dorsal portion of the disc and about one-half of the acetabulum. The posterior portions of the disc and acetabulum are furnished by the *ischia* (*Is*), fused with one another in the sagittal plane, their ventral portions by the similarly united *pubes* (*Kn*). The ilium and ischium are formed of true bone, the pubis of calcified cartilage; the union of the elements in the median plane is called the *symphysis*. In the larva the ilium is vertical, but during development it becomes lengthened and at the same time rotated backwards, thus bringing the articulation of the hind limbs as far back as possible.

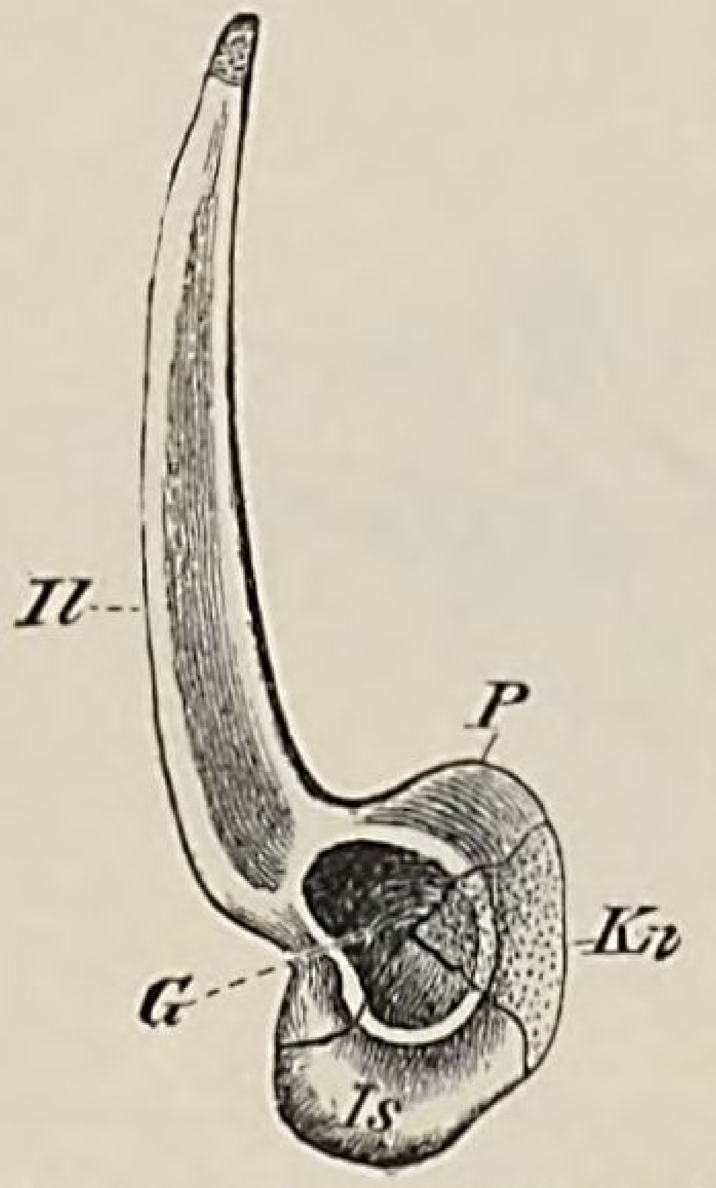


FIG. 874.—**Rana esculenta.** Pelvic girdle from the right side. *G*, acetabulum; *Il*, *P*, ilium; *Is*. ischium; *Kn*, pubis. (From Wiedersheim's *Comparative Anatomy*.)

In the *hind-limb* the tibia and fibula are fused to form a single *tibio-fibula* (Fig. 870, TI. FI), and the two bones in the proximal row of the tarsus—probably the tibiale or *astragalus* (AST) and the fibulare or *calcaneum* (CAL)—are greatly elongated and provide the leg with an additional segment. There are three tarsals in the distal row, one of which appears to represent a centrale, another the first distale, and the third the fused second and third distalia. There are five well-developed digits, and on the tibial side of the first is a spur-like structure or *calcar* (*c*), formed of three bones, a metatarsal and two phalanges: such a rudimentary digit is called a *præ-hallux*.

All the long bones of the limbs consist of a *shaft* formed of true bone and of *extremities* of calcified cartilage. The distinction is a very obvious one, both in the freshly prepared and in the dried skeleton.

The **muscular system** has undergone great modifications in correspondence with the complex movements performed by the

limbs. The dorsal muscles of the trunk are no longer divisible into myomeres, but take the form of longitudinal or oblique bands (*extensores dorsi*, &c.), lying partly above the vertebræ, partly

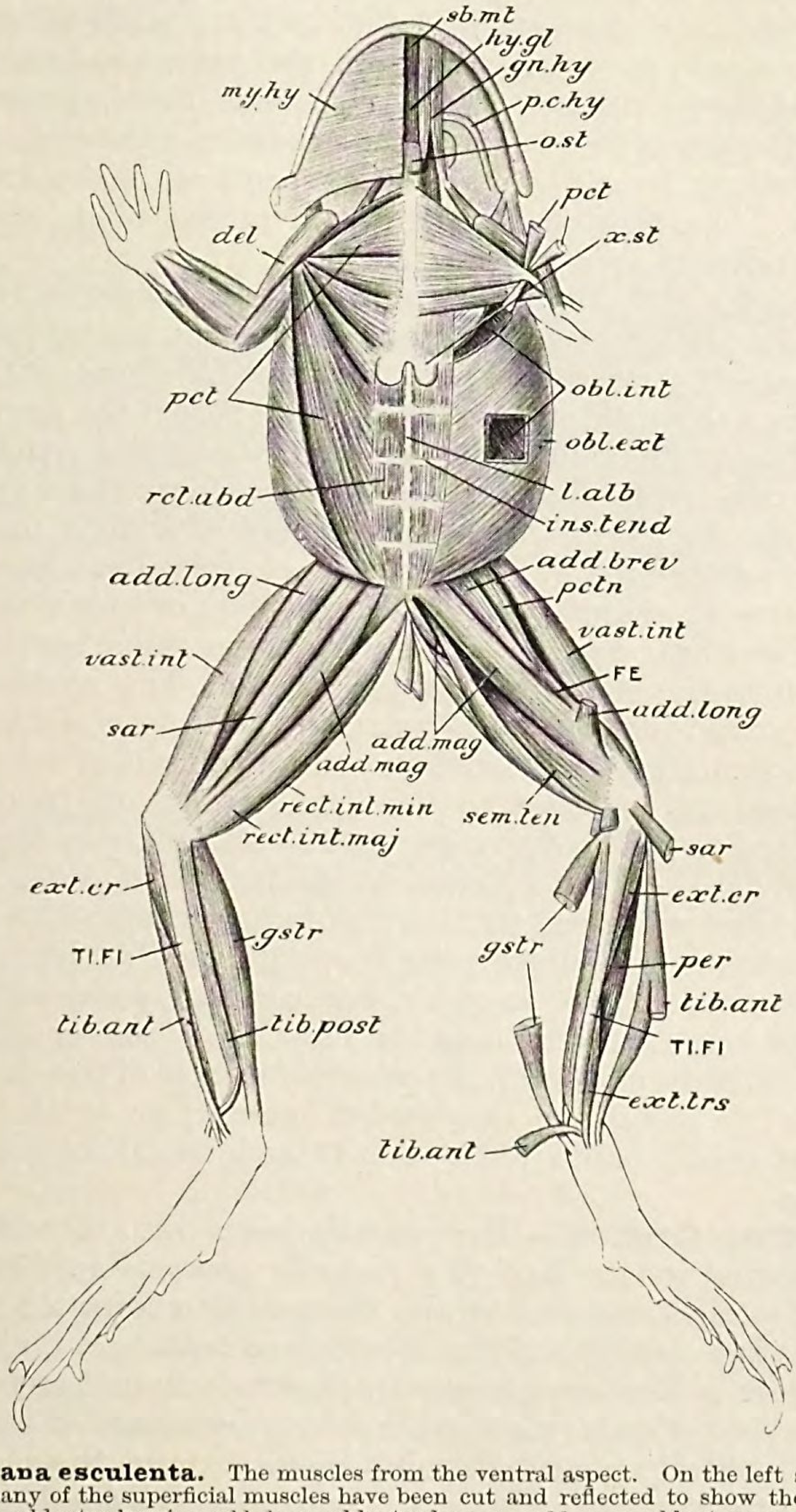


FIG. 875.—**Rana esculenta.** The muscles from the ventral aspect. On the left side (right of figure) many of the superficial muscles have been cut and reflected to show the deep layer. *add. brev.* adductor brevis; *add. long.* adductor longus; *add. mag.* adductor magnus; *del.* deltoid; *ext. cr.* extensor cruris; *ext. trs.* extensor tarsi; FE. femur; *gn. hy.* genio-hyoid; *gstr.* gastrocnemius; *hy.gl.* hyoglossus; *ins. ten.* inscriptio tendinea; *l. alb.* linea alba; *my.hy.* mylo-hyoid; *obl. int.* obliquus internus; *obl. ext.* obliquus externus; *o.st.* omosternum; *p. c. hy.* posterior cornu of hyoid; *pct.* pectoralis; *pctn.* pectineus; *per.* peronæus; *rct. abd.* rectus abdominis; *rect. int. maj.* rectus internus major; *sar.* sartorius; *sb. mt.* sub-mentalis; *sem. ten.* semi-tendinosus; *tib. ant.* tibialis anticus; *tib. post.* tibialis posticus; TI. FI. tibio-fibula; *vast. int.* vastus internus; *x. st.* xiphi-sternum.

between the transverse processes, partly between the ilia and the urostyle. The ventral muscles are differentiated into a paired median band, the *rectus abdominis* (Fig. 875, *rct. abd*) with longitudinal fibres, and a double layer of oblique fibres—*obliquus externus* (*obl. ext*) and *internus* (*obl. int*) — extending from the vertebral column to the recti. Both the extensor dorsi and the rectus abdominis are traversed at intervals by transverse bands of fibrous tissue, the *inscriptiones tendineæ* (*ins. ten*), but the segments thus formed do not correspond with the embryonic myomeres. The right and left recti are united by a longitudinal band of tendon, the *linea alba* (*l. alb*).

The muscles of the limbs are numerous and complex, each segment having its own set of muscles by which the various movements of which it is capable are performed. There are muscles passing from the trunk to the limb-girdles; from the trunk or the limb-girdles to the humerus and femur; from the humerus and femur to the radio-ulna and tibio-fibula; from the fore-arm or shank to the digits; and from one segment of a digit to another. For the most part the limb-muscles are elongated and more or less spindle-shaped, presenting a muscular portion or *belly* which passes at either end into a *tendon* of strong fibrous tissue serving to fix the muscle to the bones upon which it acts. The relatively fixed end of a muscle is called its *origin*, the relatively movable end its *insertion*, *e.g.* in the *gastrocnemius* muscle of the calf of the leg (*gstr*) the proximal end attached to the femur is the origin, the distal end attached to the foot the insertion. According to their action muscles are divided into *flexors* which bend, and *extensors* which straighten one part upon another; *adductors* which draw towards, and *abductors* which draw away from, the middle line; *elevators* which raise and *depressors* which lower a part, such as the lower jaw. The names of the muscles may have reference to their position, *e.g. pectoralis* (*pct.*), the principal muscle of the chest; or to their form, *e.g. biceps*, the two-headed muscle; or to their action, *e.g. flexor tarsi;* or to their origin and insertion, *e.g. coraco-humeralis.*

Digestive Organs.—The mouth leads into a wide *buccal cavity* having in its roof the *posterior nares* (Fig. 876, *p. na.*), a pair of projections due to the downward bulging of the large eyes, and the openings of the *Eustachian tubes* (*eus. t*, *vide infra*). On its floor is the large *tongue* (*tng*), attached in front and free behind, where it ends in a double point; by means of its muscles it can be suddenly projected, point foremost, from the mouth, and is used in the capture of Insects. Immediately behind the tongue is the *glottis* (*gl*). *Teeth* are arranged in a single series round the edge of the upper jaw, attached to the premaxillæ and maxillæ; there is also a small patch of teeth (*vo. t*) on each vomer just internal to the posterior nostril. The teeth are small conical

bodies, their bases ankylosed to the bones; their only use is to prevent the polished or slimy bodies of the prey—Insects and Worms—from slipping out of the mouth.

The buccal cavity narrows towards the *pharynx*, which leads by a short *gullet* (*gul*) into a *stomach* (*st*) consisting of a wide cardiac, and a short, narrow, pyloric division. The *duodenum* (*du*) or first portion of the small intestine passes forwards parallel with the stomach; the rest of the *small intestine* is twisted into a coil. The

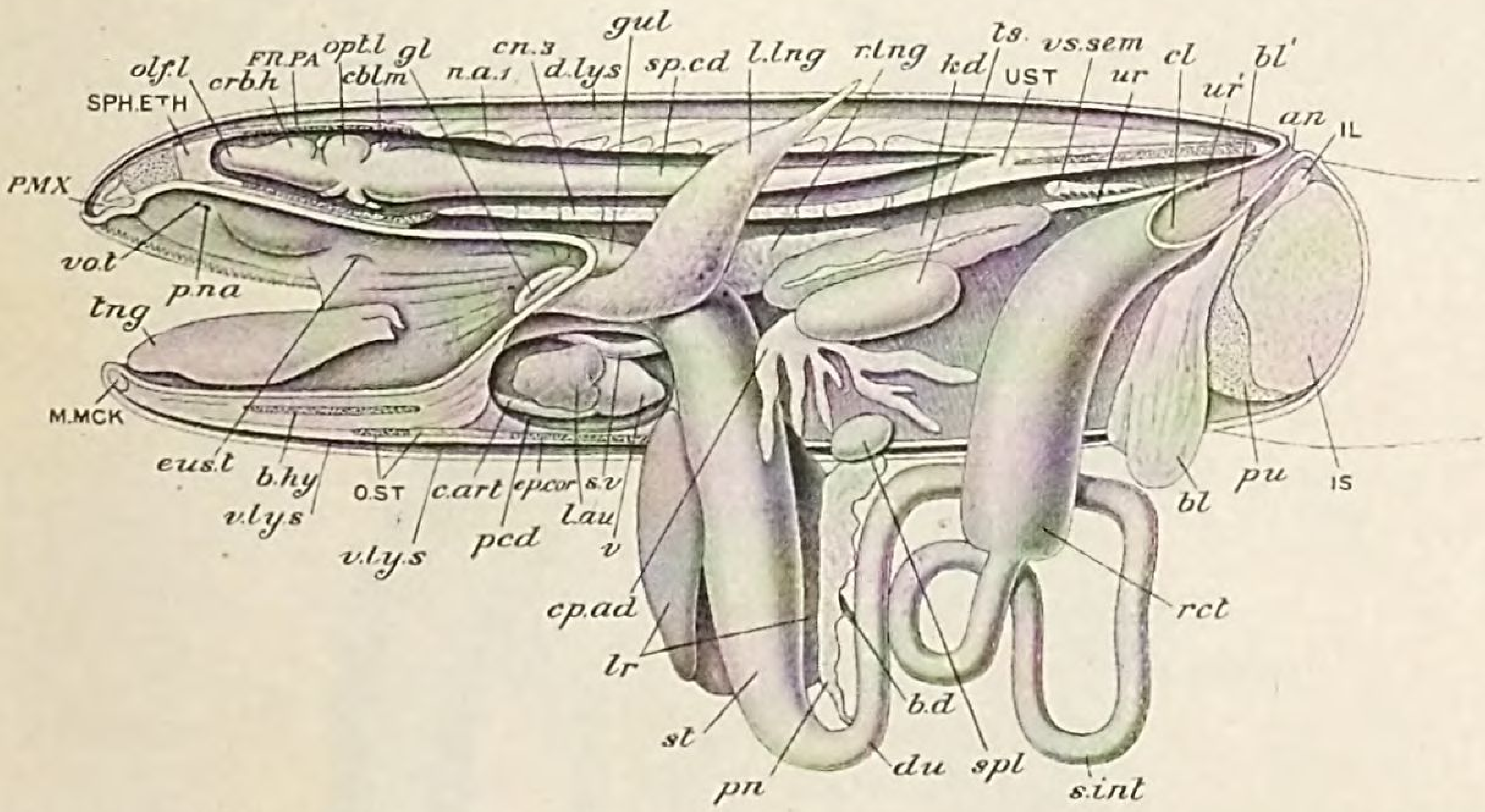


FIG. 876.—**Rana temporaria.** Dissection from the left side; the viscera somewhat displaced. *an.* anus; *b. d.* bile-duct; *b. hy.* body of hyoid; *bl.* urinary bladder; *bl.'* its opening into cloaca; *c. art.* conus arteriosus; *cblm.* cerebellum; *cl.* cloaca; *cn. 3*, centrum of third vertebra; *cp. ad.* corpus adiposum; *crb. h.* cerebral hemisphere; *d. ly. s.* dorsal lymph sinus; *du.* duodenum; *ep.cor.* epicoracoid; *eus. t.* Eustachian tube; *FR. PA.* fronto-parietal; *gl.* glottis; *gul.* gullet; IL. ilium; IS. ischium; *kd.* kidney; *l. au.* left auricle; *l. lng.* left lung; *lr.* liver; M. MCK. mento-meckelian; *n. a. 1*, neural arch of first vertebra; *olf. l.* olfactory lobe; *opt. l.* optic lobe; O. ST. omo- and epi-sternum; *pcd.* pericardium; *PMX.* premaxilla; *pn.* pancreas; *p. na.* posterior naris; *pu.* pubis; *rct.* rectum; *r. lng.* right lung; *s. int.* small intestine; *sp. cd.* spinal cord; SPH. ETH. sphenethmoid; *spl.* spleen; *st.* stomach; *s. v.* sinus venosus; *tng.* tongue; *ts.* testis; *ur.* ureter; *ur.'* its aperture into the cloaca; UST. urostyle; *v.* ventricle; *v. ly. s.* ventral lymph sinus; *vo. t.* vomerine teeth; *vs. sem.* vesicula seminalis.

large intestine or *rectum* (*rct*) is very wide and short, and passes without change of diameter into the cloaca (*cl*).

The *liver* (*lr*) is two-lobed; between the right and left lobes lies a large *gall-bladder* (Fig. 877, *G*). The *pancreas* (*P*) is an irregular gland surrounding the bile-duct, into which it pours its secretion; the *spleen* (Fig. 876, *spl*) is a small, red, globular body attached near the anterior end of the rectum. The *thyroids* are small paired organs lying below the floor of the mouth in front of the glottis. The *thymus* is also paired, and lies behind and below the tympanic membrane.

Respiratory Organs.—The *lungs* (*l. lng*, *r. lng*) are elastic sacs lying in the anterior part of the cœlome above the heart and liver; their size and appearance vary greatly according to their state of distension. Each contains a spacious cavity and has its walls

raised into a complex network of ridges abundantly supplied with blood-vessels. The two lungs open anteriorly into a small *laryngo-tracheal chamber* which communicates with the mouth by the narrow slit-like *glottis*. The walls of the laryngo-tracheal chamber are supported by a cartilaginous framework, and its mucous membrane is raised into a pair of horizontal folds, the

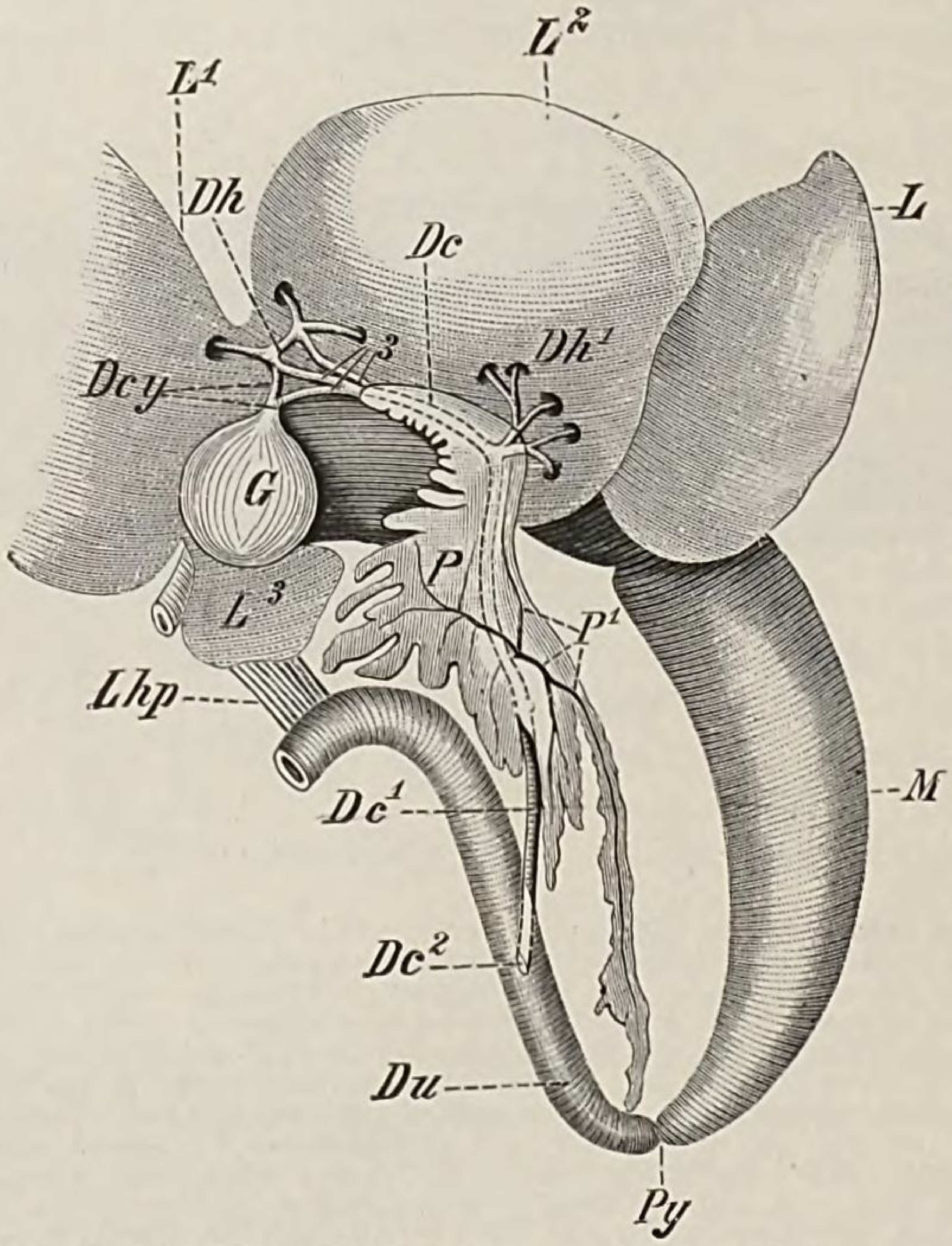


FIG. 877.—**Rana esculenta.** Stomach and duodenum with liver and pancreas. *Dc.*, *Dc*¹. common bile duct; *Dc.*² its opening into the duodenum; *d. cy.* cystic ducts; *Dh.*, *Dh.*¹ hepatic ducts; *Dn.* duodenum; *G.* gall-bladder; *L*, *L*¹, *L*², *L*³, lobes of liver, turned forwards; *Lhp.* duodeno-hepatic omentum, a sheet of peritoneum connecting the liver with the duodenum; *M*, stomach; *P.* pancreas; *P*¹, pancreatic duct; *Py.* pylorus. (From Wiedersheim's *Comparative Anatomy*.)

vocal chords, by the vibration of which the croak of the Frog is produced.

In breathing, the Frog keeps its mouth closed, and, by depressing the floor of the mouth, draws air into the buccal cavity through the nostrils. The floor of the mouth is then raised, the nostrils, which are valvular, are closed, and the air is forced through the glottis into the lungs. The skin also is an important respiratory organ.

Circulatory Organs.—The *pericardium* (Fig. 876, *pcd.*) is not a separate chamber, as in Fishes, but lies in the general cœlomic cavity between the gullet above and the epicoracoids below; it

consists, as usual, of a visceral layer closely adherent to the heart, and a loose parietal layer, the two being continuous at the bases of the great vessels and separated by a small quantity of pericardial fluid.

The *heart* consists of a sinus venosus (Figs. 876 and 880, *s. v.*), right and left auricles (*r. au.*, *l. au.*), a ventricle (*v.*, *vt.*), and a conus arteriosus (*c. art.*). As in Dipnoi, the sinus venosus opens into the right auricle, the pulmonary veins into the left; a striking advance

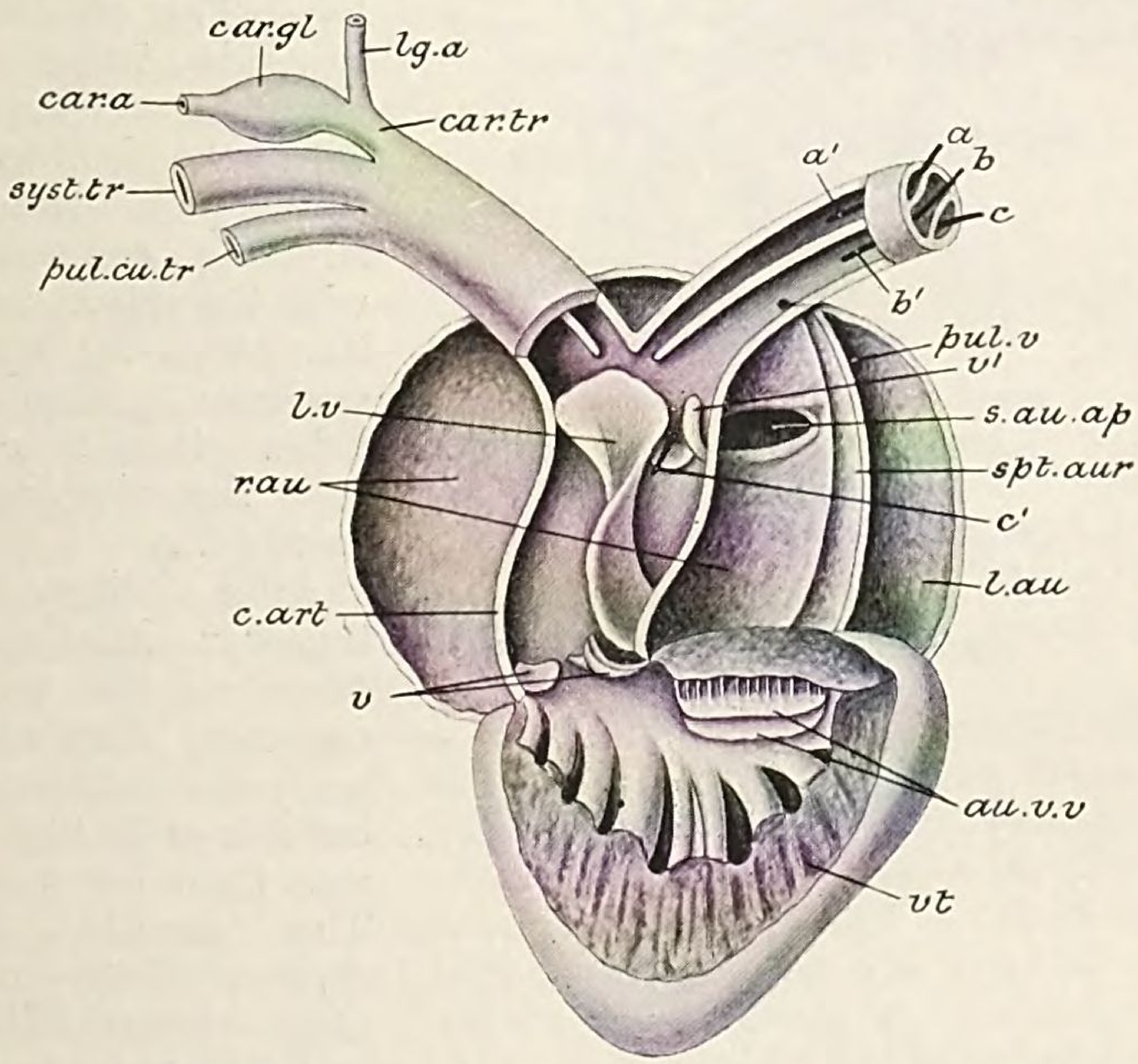


FIG. 878.—**Rana temporaria.** The heart from the ventral aspect with the cavities laid open. *a*, *a′*, bristle in left carotid trunk; *au. v. v.* auriculo-ventricular valves; *b. b′.* bristle in left systemic trunk; *c*, *c′*, bristle in left pulmo-cutaneous trunk; *car. a.* carotid artery; *car. gl.* carotid plexus; *c. art.* conus arteriosus; *car. tr.* carotid trunk; *l. au.* left auricle; *lg. a.* lingual artery; *l. v.* longitudinal valve; *pul. cu. tr.* pulmo-cutaneous trunk; *pul. v.* aperture of pulmonary veins; *r. au.* right auricle; *s. au. ap.* sinu-auricular aperture; *spt. aur.* septum auricularum; *v. v′.* valves; *vt.* ventricle.

is seen in the greatly increased size of the left auricle and its separation by a complete partition, the *septum auricularum* (Fig. 878, *spt. aur.*), from the right. The two auricles open by a common auriculo-ventricular aperture, guarded by a pair of valves (*au. v. v.*), into the single ventricle. The conus springs from the right side of the base of the ventricle; it is separated from the latter by three small semilunar valves (*v.*), and is traversed obliquely along its whole length by a large flap-like longitudinal valve (*l. v.*) which springs from its dorsal wall and is free ventrally. The conus passes without change of diameter into a *bulbus aortæ*, the two being separated by

S 2

a semilunar valve (v'.) and by the free end of the longitudinal valve The bulbus gives off two branches, right and left, each of them divided by two longitudinal partitions into three vessels, an inner or anterior, the *carotid trunk* (*car. tr.*), a middle, the *systemic trunk* or *aortic arch*, and an outer or posterior, the *pulmo-cutaneous trunk* (*pul. cu. tr.*). The carotid and systemic trunks communicate separately with the bulbus, the two pulmo-cutaneous trunks communicate with the anterior end of the conus by a single aperture placed just below the free end of the longitudinal valve (c'.).

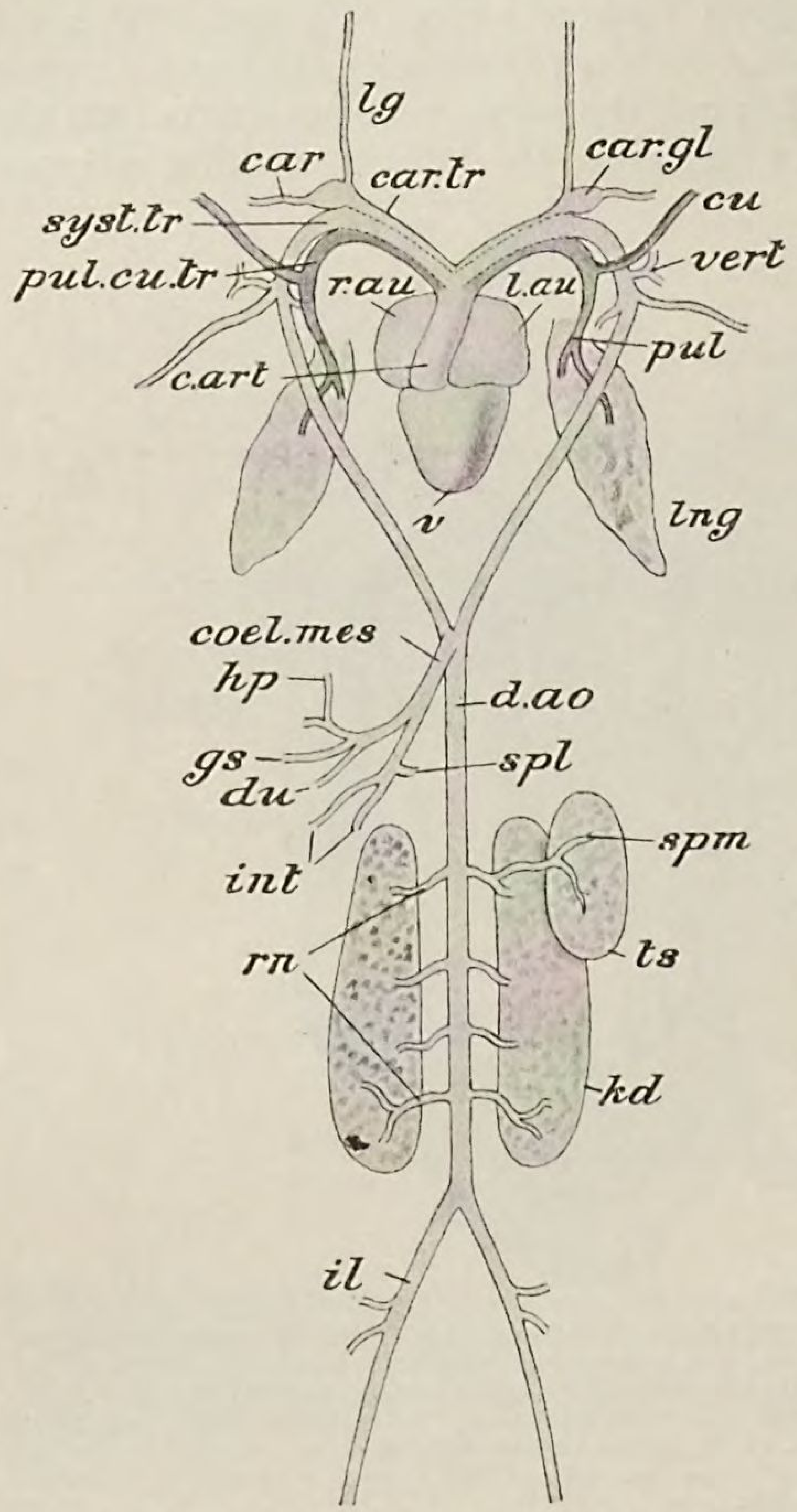


FIG. 879.—**Rana temporaria.** The arterial system, with the heart, lungs, kidneys, and left testis, from the ventral aspect. *car.* carotid artery; *car. gl.* carotid gland; *c. art.* conus arteriosus; *car. tr.* carotid trunk; *cœl. mes.* cœliaco-mesenteric artery; *cu.* cutaneous artery; *d. ao.* dorsal aorta; *du.* duodenal artery; *gs.* gastric artery; *hp.* hepatic artery; *il.* iliac artery; *int.* intestinal arteries; *kd.* kidney; *l. au.* left auricle; *lg.* lingual artery; *pul.* pulmonary artery; *pul. cu. tr.* pulmo-cutaneous trunk; *r. au.* right auricle; *rn.* renal arteries; *spl.* splenic artery; *syst. tr.* systemic trunk; *spm.* spermatic artery; *ts.* testis; *v.* ventricle.

After being bound together in the way described for a short distance, the carotid, systemic, and pulmo-cutaneous trunks separate from one another. The carotid trunk divides into *carotid* (Figs. 878 and 879, *car.*) and *lingual* (*lg.*) *arteries* for the supply of the head, the former having at its base a small swelling, the *carotid gland* (*car. gl.*), consisting of a plexus of blood-vessels. The systemic trunks curve round the gullet and unite with one another above it to form the *dorsal aorta* (*d. ao.*), from which, or from one of the systemic trunks themselves, the arteries to all parts of the body, except the head, the lungs, and the skin, are given off. The pulmo-cutaneous trunk divides into two, a

pulmonary artery (*pul.*) to the lung, and a *cutaneous artery* (*cu.*) to the skin.

In the Tadpole there are four aortic arches, each consisting of an afferent and an efferent branchial artery connected by the capillaries of the gills. As the water-breathing larva undergoes metamorphosis into the air-breathing adult the gills disappear; the first aortic arch loses its connection with the dorsal aorta and becomes the carotid trunk; the second enlarges, retains its connection with the dorsal aorta, and becomes the systemic trunk; the third disappears; and the fourth sends off branches to the lungs and skin, loses its connection with the dorsal aorta, and becomes the pulmo-cutaneous trunk.

The blood from each side of the head is returned by *internal* (Fig. 880, *int. ju.*) and *external* (*ext. ju.*) *jugular veins* into the *precaval vein* (*pr. v.*), which also receives the *brachial vein* (*br.*) from the fore-limb, and the *musculo-cutaneous vein* (*ms. cu.*) from the skin and muscles of the side and back, and part of the head. The two precavals open separately into the sinus venosus.

The course of the blood from the posterior parts of the body is very different from what we have met with in Fishes, the differences being due partly to the absence of a tail, partly to a peculiar modification of the lateral veins, and partly to the substitution of the cardinals by a *post-caval vein*, found among Fishes only in the Dipnoi.

The blood from the front part of the hind leg is brought back by a *femoral vein* (*fm.*) which, on reaching the cœlome, divides into two branches, a dorsal and a ventral. The dorsal branch is the *renal portal vein* (*rn. pt.*): it receives the *sciatic vein* (*sc.*) from the back of the leg and passes to the kidney, when it breaks up into capillaries. The ventral branch is the *pelvic vein* (*pv.*): it unites with its fellow of the opposite side to form the *abdominal vein* (*abd.*) which passes forwards in the ventral body-wall, between the linea alba and the peritoneum, to the level of the sternum, where it turns inwards and divides into two branches, both breaking up into capillaries in the liver. Just as it enters the liver it is joined by the *hepatic portal vein* (*hp. pt.*), bringing the blood from the stomach, intestine, spleen, and pancreas. The abdominal vein also receives *vesical veins* (*ves.*) from the urinary bladder, and a small *cardiac vein* from the heart (*cd.*). It represents the lateral veins of Elasmobranchs united in the middle ventral line: the pelvic veins are their posterior free portions.

The blood is collected from the kidneys by the *renal veins* (*rn.*), which unite to form the large unpaired *postcaval vein* (*pt. cv.*). This passes forwards through a notch in the liver, receives the *hepatic veins* (*hp.*) from that organ, and finally opens into the sinus venosus. Thus the blood from the hind limbs has to pass through one of the two portal systems on its way back to the heart: part of it goes by the renal portal veins to the kidneys, and thence by

the renal veins to the post-caval, part by the pelvic and abdominal veins to the liver, and thence by the hepatic veins to the post-caval. Lastly, the blood which has been purified in the lungs is returned by the *pulmonary veins* (*pul.*) directly to the left auricle.

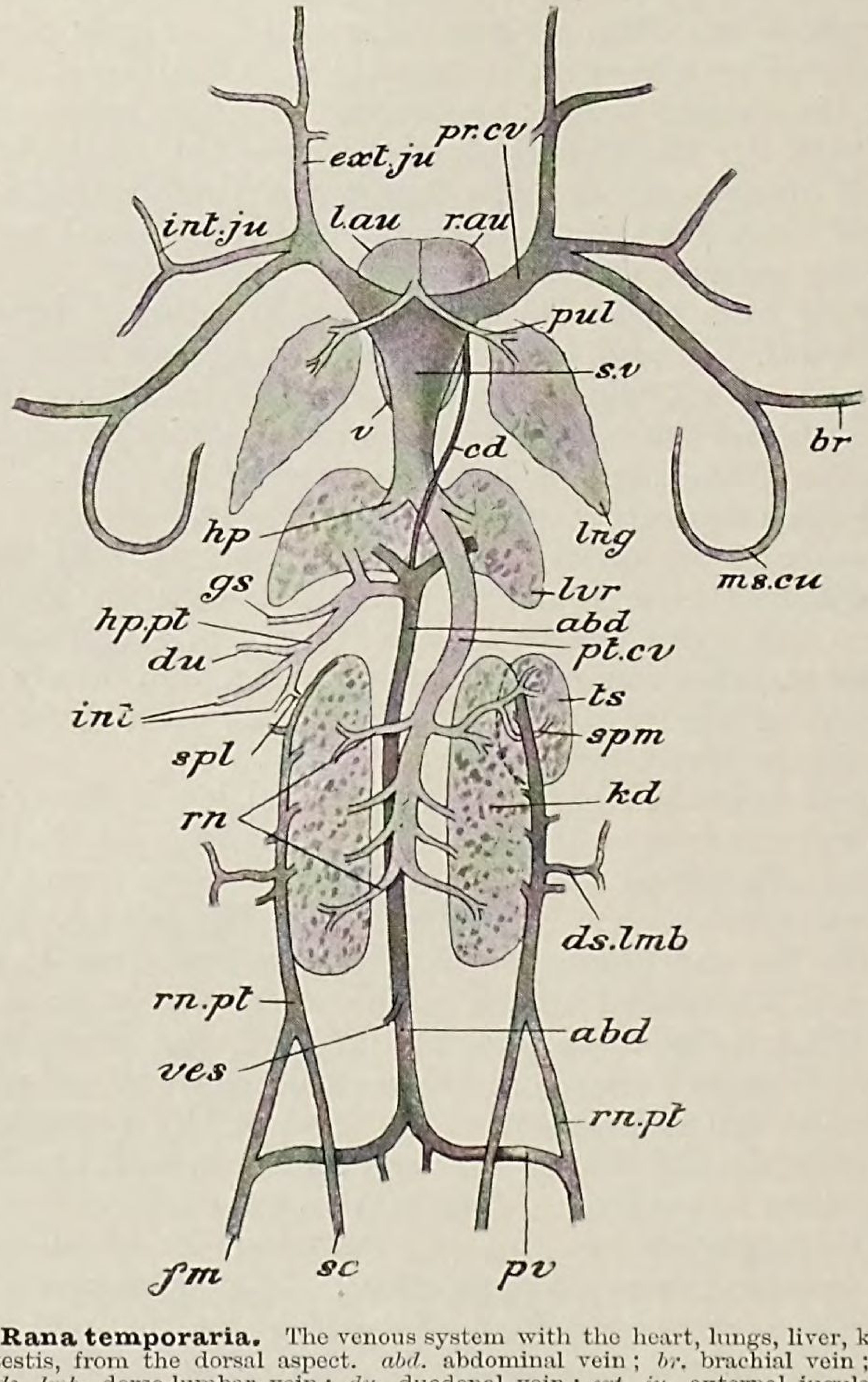


FIG. 880.—**Rana temporaria.** The venous system with the heart, lungs, liver, kidneys, and right testis, from the dorsal aspect. *abd.* abdominal vein; *br.* brachial vein; *cd.* cardiac vein; *ds. lmb.* dorso-lumbar vein; *du.* duodenal vein; *ext. ju.* external jugular vein; *fm.* femoral vein; *gs.* gastric vein; *hp.* hepatic vein; *hp. pt.* hepatic portal vein; *int.* intestinal veins; *int. ju.* internal jugular vein; *kd.* kidney; *l. au.* left auricle; *lng.* lung; *lvr.* liver; *ms. cu.* musculo-cutaneous vein; *pr. cv.* precaval vein; *pt. cv.* post-caval vein; *pul.* pulmonary vein; *pv.* pelvic vein; *r. au.* right auricle; *rn.* renal veins: *rn. pt.* renal portal vein; *sc.* sciatic vein; *spl.* splenic vein; *spm.* spermatic vein; *s. v.* sinus venosus; *ts.* testis; *ves.* vesical veins.

It will be seen that there is no trace of cardinal veins in the Frog: these are, however, present in the larva, but, during metamorphosis, their posterior ends become united with the post-caval, and their anterior ends disappear altogether.

It will be perceived that the blood poured into the right auricle is mostly impure or venous, that poured into the left fully aërated or arterial. When the auricles contract, which they do simultaneously, each passes its blood into the corresponding part of the ventricle, which then instantly contracts, before the venous and arterial bloods have time to mix. Since the conus arteriosus springs from the right side of the ventricle, it will at first receive only venous blood, which, on the contraction of the conus, might pass either into the bulbus aortæ or into the aperture of the pulmo-cutaneous trunks. But the carotid and systemic trunks are connected with a much more extensive capillary system than the pulmo-cutaneous, and the pressure in them is proportionally great, so that it is easier for the blood to enter the pulmo-cutaneous trunks than to force aside the valves between the conus and the bulbus. A fraction of a second is, however, enough to get up the pressure in the pulmonary and cutaneous arteries, and in the meantime the pressure in the arteries of the head, trunk, &c., is constantly diminishing, owing to the continual flow of blood towards the capillaries. Very soon, therefore, the blood forces the valves aside and makes its way into the bulbus aortæ. Here again the course taken is that of least resistance: owing to the presence of the carotid gland the passage of blood into the carotid trunks is less free than into the wide, elastic, systemic trunks. These will therefore receive the next portion of blood, which, the venous blood having been mostly driven to the lungs, will be a mixture of venous and arterial. Finally, as the pressure rises in the systemic trunks the last portion of blood from the ventricle, which, coming from the left side, is arterial, will pass into the carotids and so supply the head.

The *red blood-corpuscles* are, like those of Fishes, oval, nucleated discs. The *lymphatic system* is very well developed, and is remarkable for the dilatation of many of its vessels into immense *lymph sinuses.* Between the skin and muscle are large *subcutaneous sinuses* (Fig. 876, *v. ly. s.*), separated from one another by fibrous partitions, and the dorsal aorta is surrounded by a spacious *subvertebral sinus.* The lymph is pumped into the veins by two pairs of *lymph-hearts*, one situated beneath the supra-scapulæ, the other beside the posterior end of the urostyle.

Nervous system.—The *brain* (Fig. 881), has a very small cerebellum (*HH*), large optic lobes (*MH*), a well-developed diencephalon, and large hemispheres and olfactory lobes, the latter fused in the median plane. The optic thalami are connected with one another by *anterior* and *posterior commissures* (*co. a.*, *co. p.*), and above the former is a transverse band of fibres (*co.s.*) which probably represents the *hippocampal commissure* of the mammalian brain. The metacœle (*V. iv.*) is covered by a thick choroid plexus: the mesocœle is divisible into a median passage or *iter* (*Aq. Syl.*) and paired *optocœles* in the optic lobes: the paracœles are large

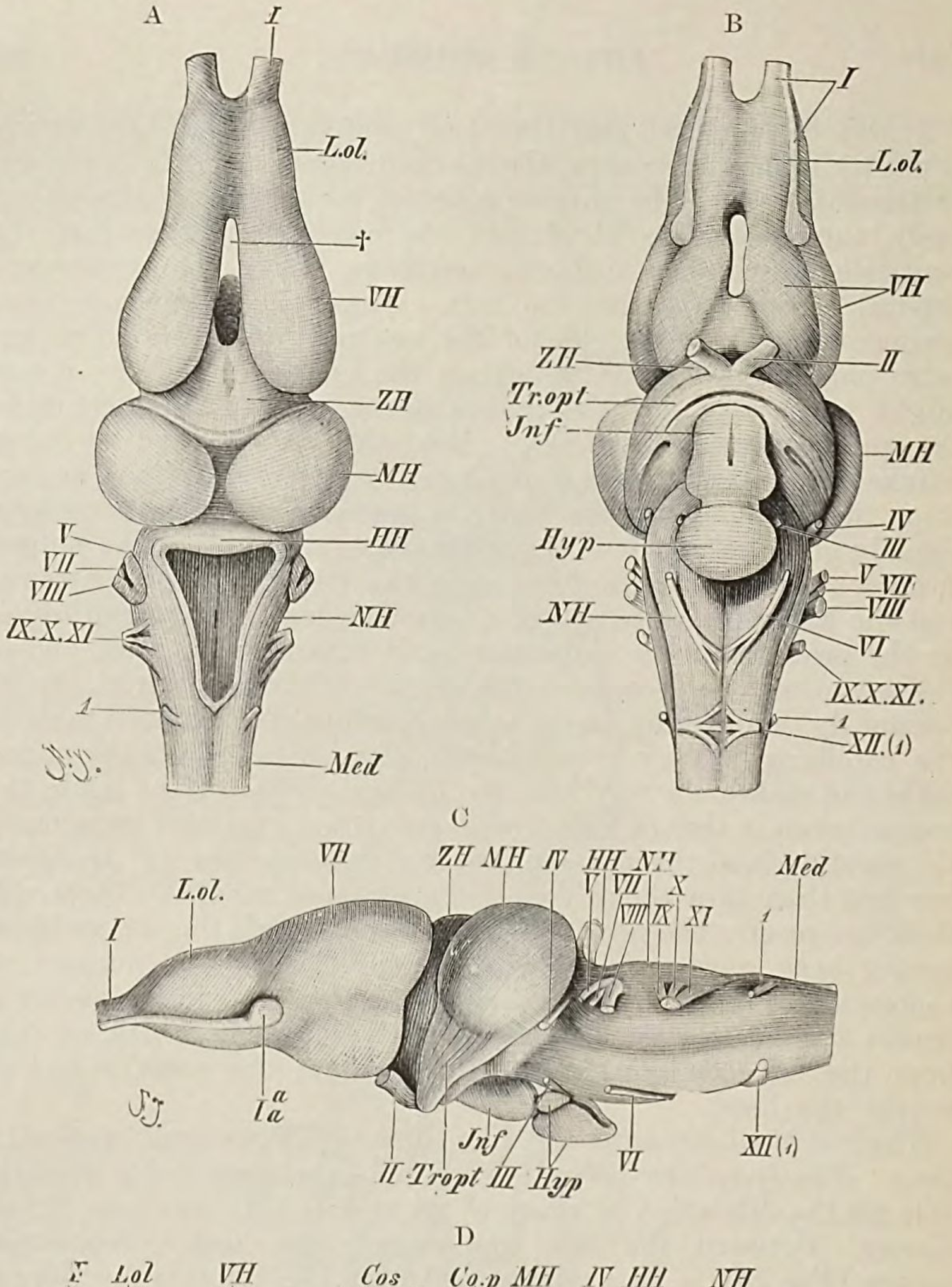


Fig. 881.—**Rana esculenta.** The brain. A, from above; B, from below; C, from the side; D, in sagittal section. *Aq. Syl.* iter or Aqueduct of Sylvius; *Ca.* corpus callosum; *ch. opt.* optic chiasma; *co. a.* anterior commissure; *co. p.* posterior commissure; *co. s.* superior commissure; *F. Mo.* foramen of Monro; *HH*, cerebellum; *Hyp.* pituitary body; *Inf.* infundibulum; *L. ol.* olfactory lobe; *Med.* spinal cord; *MH*, mid-brain; *NH*, medulla oblongata; *Th. opt.* optic thalamus; *Tr. opt.* optic tract; *V. iii.* diacœle; *V. iv.* metacœle; *VH*, cerebral hemisphere; *ZH*, diencephalon; *I—X*, cerebral nerves; *XII* (*1*), hypoglossal (first spinal) [nerve. From Wiedersheim's *Comparative Anatomy*.)

cavities each communicating with a rhinocœle in the corresponding olfactory lobe. The pineal body is absent in the adult, its place being taken by a lobe of the anterior choroid plexus: in the larva it is found outside the skull and immediately beneath the skin.

The first spinal nerve performs the function of the hypoglossal (Fig. 734, p. 98), supplying the muscles of the tongue: it passes out between the first and second vertebræ. The spinal cord is short and ends in a delicate filament, the *filum terminale.* In correspondence with the number of vertebræ there are only ten pairs of spinal nerves, of which the second and third unite to form a *brachial plexus* giving off the nerves to the fore-limb, while the seventh to the tenth join to form a *lumbo-sacral plexus* giving off the nerves to the hind-limb.

Sensory Organs.—The *olfactory sacs* have each two openings: the *anterior naris* or external nostril and the *posterior naris*

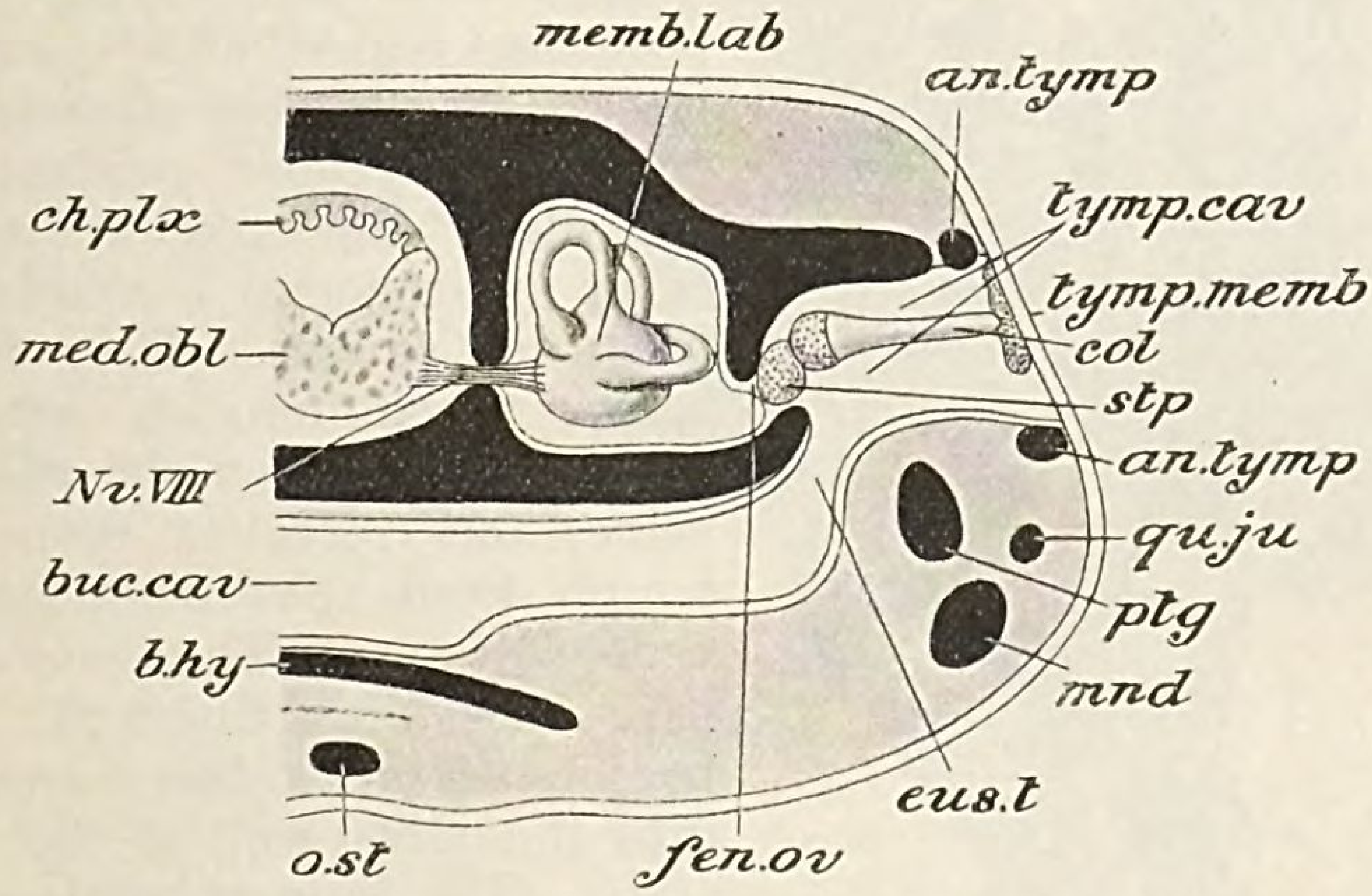


FIG. 882.—Transverse section of head of **Frog** to show the relations of the accessory auditory apparatus (diagrammatic). Skeletal structures black, with the exception of the columella; *an. tymp.* annulus tympanicus; *b. hy.* body of hyoid; *buc. cav.* buccal cavity; *ch. plx.* choroid plexus; *col.* columella; *eus. t.* Eustachian tube; *fen. ov.* fenestra ovalis; *med. obl.* medulla oblongata; *memb. lab.* membranous labyrinth; *mnd.* mandible; *Nv. VIII.* auditory nerve; *o. st.* epi-sternum; *ptg.* pterygoid; *qu. ju.* quadrato-jugal; *stp.* stapes; *tymp. cav.* tympanic cavity; *tymp. m.* tympanic membrane.

(Fig. 876, *p. na.*) or internal nostril, which opens into the mouth immediately external to the vomer.

The *eye* and the *auditory organ* have the usual structure, but in connection with the latter there is an important accessory organ of hearing not hitherto met with. Bounded externally by the tympanic membrane and internally by the outer wall of the auditory capsule is a considerable space, the *tympanic cavity* (Fig. 882, *tymp. cav.*), which communicates with the mouth by the short Eustachian tube (*eus. t.*) already noticed (Fig. 876, *eus. t.*), so that a probe thrust through the tympanic membrane from outside passes directly into the mouth. In the roof of the tympanic cavity lies the columella (*col.*), its head, or extra-columella, attached to the inner

surface of the tympanic membrane, its handle united to the stapes (*stp.*), which is fixed in the membrane of the fenestra ovalis (*fen. ov.*). Sonorous vibrations striking the tympanic membrane are communicated by the columella and stapes to the fenestra ovalis, thence to the perilymph, and thence to the membranous labyrinth. The connection of the Eustachian tube with the mouth obviates undue compression of the air in the tympanic cavity. There seems little doubt that the tympano-Eustachian passage is homologous with the first or hyomandibular gill-cleft, although, in the Frog, it is formed independently of the clefts and never opens on the exterior.

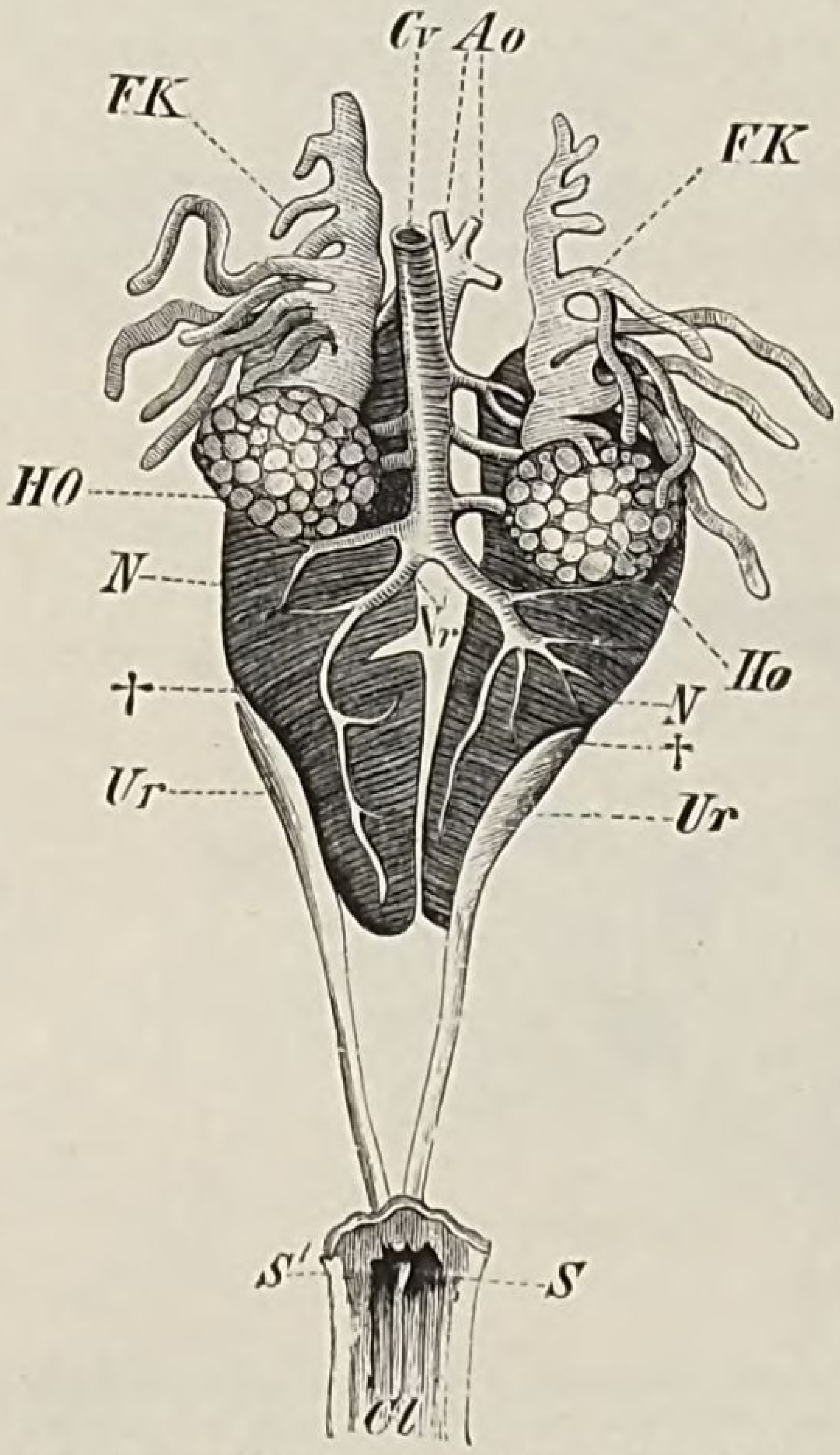


FIG. 883.—**Rana esculenta.** Urinogenital organs of the male. *Ao.* dorsal aorta; *Cl.* cloaca; *Cv.* post-caval vein; *FK*, fat bodies; *HO.* testes; *N*, kidneys; *S*, apertures of ureters into cloaca; *Ur.* ureters. (From Wiedersheim's *Comparative Anatomy*.)

Urinogenital Organs.—The *kidneys* (Figs. 883 and 884, *N.*), are flat, somewhat oval bodies of a dark red colour, lying in the posterior region of the cœlome. On the ventral face of each is an elongated, yellow *adrenal*, and irregularly scattered *nephrostomes* occur in considerable numbers on the same surface. They do not, however, communicate with the urinary tubules, but with the renal veins, and serve to propel the lymph from the cœlome to the venous system. The *ureters* (*Ur.*) pass backwards from the outer borders of the kidneys and open into the dorsal wall of the cloaca (*Cl.*). The kidney is developed from the mesonephros of the embryo, the ureter from the mesonephric duct. In the larva a large pronephros is present and is, for a time, the functional kidney.

Opening into the cloaca on its ventral side is an organ (Fig. 876, *bl.*) mentioned in the general account of the Craniata (p. 113), but here actually met with for the first time. It is a bilobed, thin-walled, and very delicate sac into which the urine passes by gravitation from the cloaca when the anus is closed. The sac is a *urinary bladder*, but as it is quite different morphologically from the organ of the same name in Fishes, which is a dilatation of the ureter, it is distinguished as the *allantoic bladder*.

The *testes* (*HO.*) are white ovoid bodies lying immediately ventral to the anterior ends of the kidneys, to which they are attached by folds of peritoneum. From the inner edge of each pass a number

of delicate *vasa efferentia* which enter the kidney and become connected with the urinary tubules. The spermatic fluid is thus passed into the urinary tubules and carried off by the ureter, which is therefore a urinogenital duct in the male Frog. A *vesicula seminalis* (Fig. 876, *vs. sem.*) opens by numerous small ducts into the outer side of the ureter. Attached to the testis are lobed bodies of a bright yellow colour, the *fat-bodies* (*FK*).

The *ovaries* (Fig. 884, *Ov.*) are large folded sacs on the surface of which the black and white ova project. A fat-body is attached to each. The *oviducts* (*Od.*) are greatly convoluted tubes, the narrow anterior ends of which open into the cœlome by small apertures (*Ot.*) placed close to the bases of the lungs. Their posterior ends are wide and thin-walled (*Ut.*) and open into the cloaca (*P*). The ova break loose from the surface of the ovary and enter the cœlomic apertures of the oviducts, the walls of which are glandular and secrete an albuminous fluid having the property of swelling up in water. The eggs receive a coating of this substance as they pass down the oviducts and are finally stored up in the thin-walled posterior portions of those tubes, which, in the breeding season, become immensely dilated and serve as uteri.

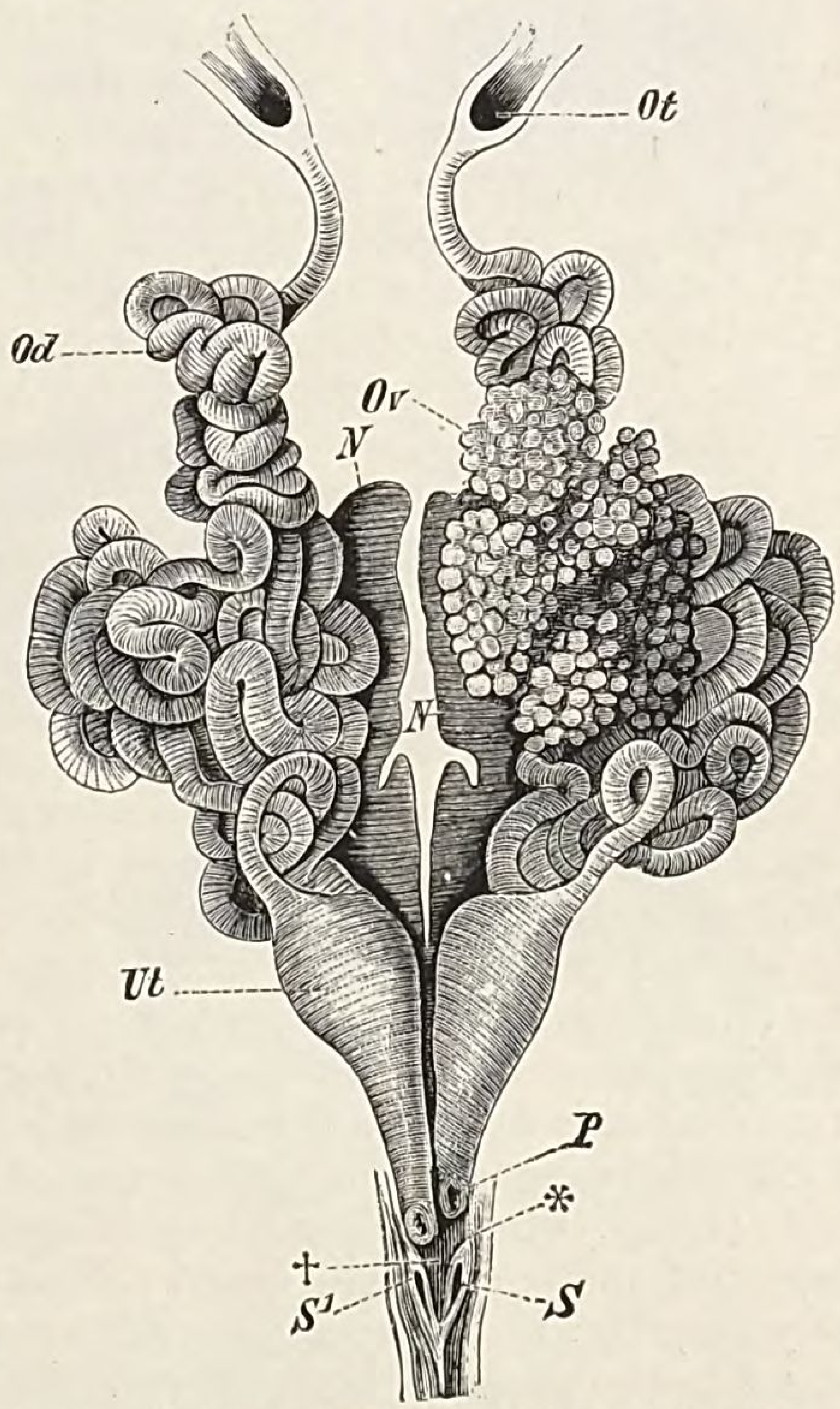


Fig. 884.—**Rana esculenta.** Urinogenital organs o the female. *N*, kidneys ; *Od.* oviduct ; *Ot*, its cœlomic aperture ; *Ov.* left ovary (the right is removed); *P*, cloacal aperture of oviduct ; *S*, *S'*, cloacal apertures of ureters ; *Ut.* uterine dilatation of oviduct. (From Wiedersheim's *Comparative Anatomy*.)

Development.—The eggs are laid in water in large masses ; each has one black and one white hemisphere, the former always directed upwards, and is surrounded by a sphere of jelly. The egg is telolecithal, the protoplasm being mainly accumulated on the pigmented hemisphere, while the white hemisphere is loaded with yolk. During oviposition the male sheds his spermatic fluid

over the eggs, and the sperms make their way through the jelly and impregnate them. In a short time the jelly swells up and becomes opaque and is thereafter impermeable to the sperms.

Segmentation begins by a vertical furrow dividing the oosperm into two cells (Fig. 885, A) and soon followed by a second vertical furrow at right angles to the first (B), and then by an equatorial furrow placed nearer the black than the white pole (C). Thus the eight-celled embryo consists of four smaller black cells and four larger white cells. Further divisions take place (D), the black cells dividing rapidly into micromeres (*mi.*), the white, more slowly, into megameres (*mg.*): as in previous cases, the presence of yolk hinders the process of segmentation. The pigmented micromeres (D—F, *mi.*) give rise to the ectoderm, which is many-layered: the megameres (*mg.*) contribute to all three layers and are commonly called *yolk-cells.* During the process of segmentation a *blastocœle* (E, *bl. cœl.*) or segmentation-cavity appears in the upper hemisphere.

The black now begins to encroach on the white hemisphere; cells, budded from the yolk-cells, take on the character of ectoderm, acquire pigment, and gradually extend the black area until it covers the whole embryo except a small patch, known as the *yolk-plug* (G, H, *yk. pl.*), at what will become the posterior end. This process is obviously one of epiboly: the margin of ectoderm cells surrounding the yolk-plug represents the blastopore.

The *archenteron* (I, *ent.*) arises by a split taking place among the yolk-cells, beginning at the edges of the blastopore and gradually extending forwards: the process is probably supplemented by a limited amount of invagination of the ectoderm. The archenteron is at first a very narrow cleft, but soon widens considerably: for a long time it does not actually communicate with the exterior, the blastopore being filled up with the yolk-plug. As the archenteron extends forwards the blastocœle gradually disappears. The yolk-cells soon become differentiated into a layer of endoderm cells (I, *end.*) immediately surrounding the archenteron, and several layers of mesoderm cells (*mes.*). Ventrally, however, a large mass of yolk-cells (K, *yk.*) remains undifferentiated and serves as nutriment to the growing embryo.

The edges of the lower margin of the blastopore now begin to approach one another, and, uniting in the median plane, give rise to a vertical groove, the *primitive groove.* In the meantime *medullary folds* (H, *md. f.*) appear and mark the dorsal surface: they are at first widely separated, but gradually approach one another and close over the medullary groove (*md. gr.*), thus giving rise to the central nervous system. Posteriorly they become continuous with the lips of the blastopore, so that when the neural groove becomes closed in behind, the archenteron, as in Amphioxus, communicates with the neurocœle by a *neurenteric canal* (K, *n.e.c.*).

The embryo soon begins to elongate; one end is broad and,

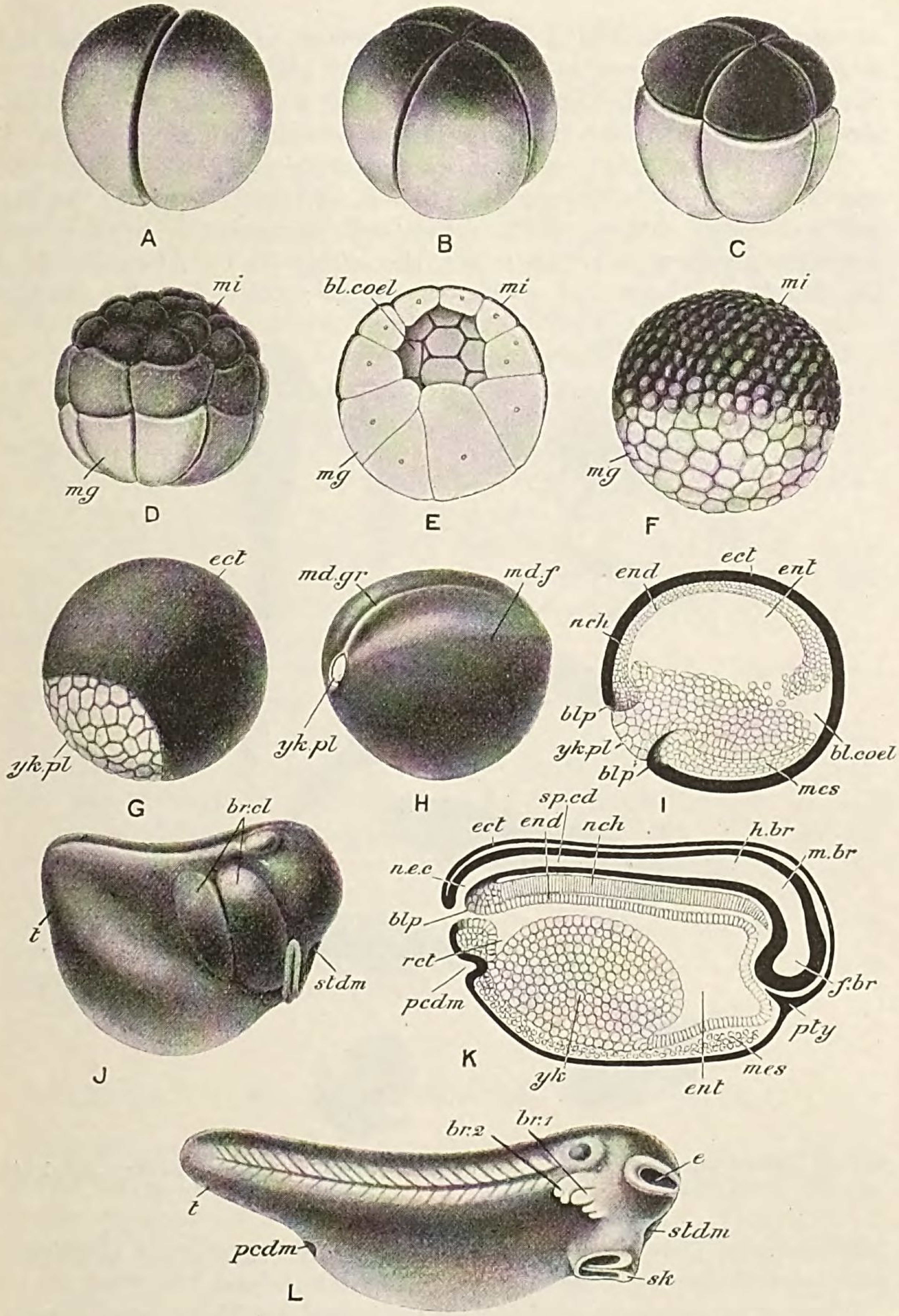


FIG. 885.—Development of the **Frog**. A—F, segmentation; G, overgrowth of ectoderm; H, I, establishment of germinal layers; J, K, assumption of tadpole-form and establishment of nervous system, notochord, and enteric canal; L, newly-hatched tadpole. *bl.cœl.* blastocœle; *blp. blp'.* blastopore; *br¹. br².* gills; *br. cl.* depressions marking position of future gill-clefts; *e.* eye; *ect.* ectoderm; *end.* endoderm; *ent.* enteron; *f. br.* fore-brain; *h. br.* hind-brain; *m. br.* mid-brain; *md. f.* medullary fold; *md. gr.* medullary groove; *mes.* mesoderm; *mg.* megameres; *mi.* micromeres; *nch.* notochord; *n. e. c.* neurenteric canal; *pcdm.* proctodæum; *pty.* pituitary invagination; *rct.* commencement of rectum; *sk.* sucker; *sp. cd.* spinal cord; *st.dm.* stomodæum; *t.* tail; *yk.* yolk cells; *yk. pl.* yolk plug. (A—D, F—H, and J from Ziegler's models; E, I, K, and L after Marshall.)

becoming separated by a slight constriction, is marked out as the *head:* the other end is bluntly pointed and is the rudiment of the *tail* (*t.*). On the ventral surface of the root of the tail a *proctodæum* (*pcdm.*) appears and communicates with the archenteron.

The head and tail become more distinctly marked off from the trunk. A pit—the *stomodæum* (J—L, *st. dm.*)—appears on the antero-ventral surface of the head, and, immediately behind it, a semilunar area with raised edges, the *sucker* (*sk.*). At each side of the head two branched processes appear; they are the *external*

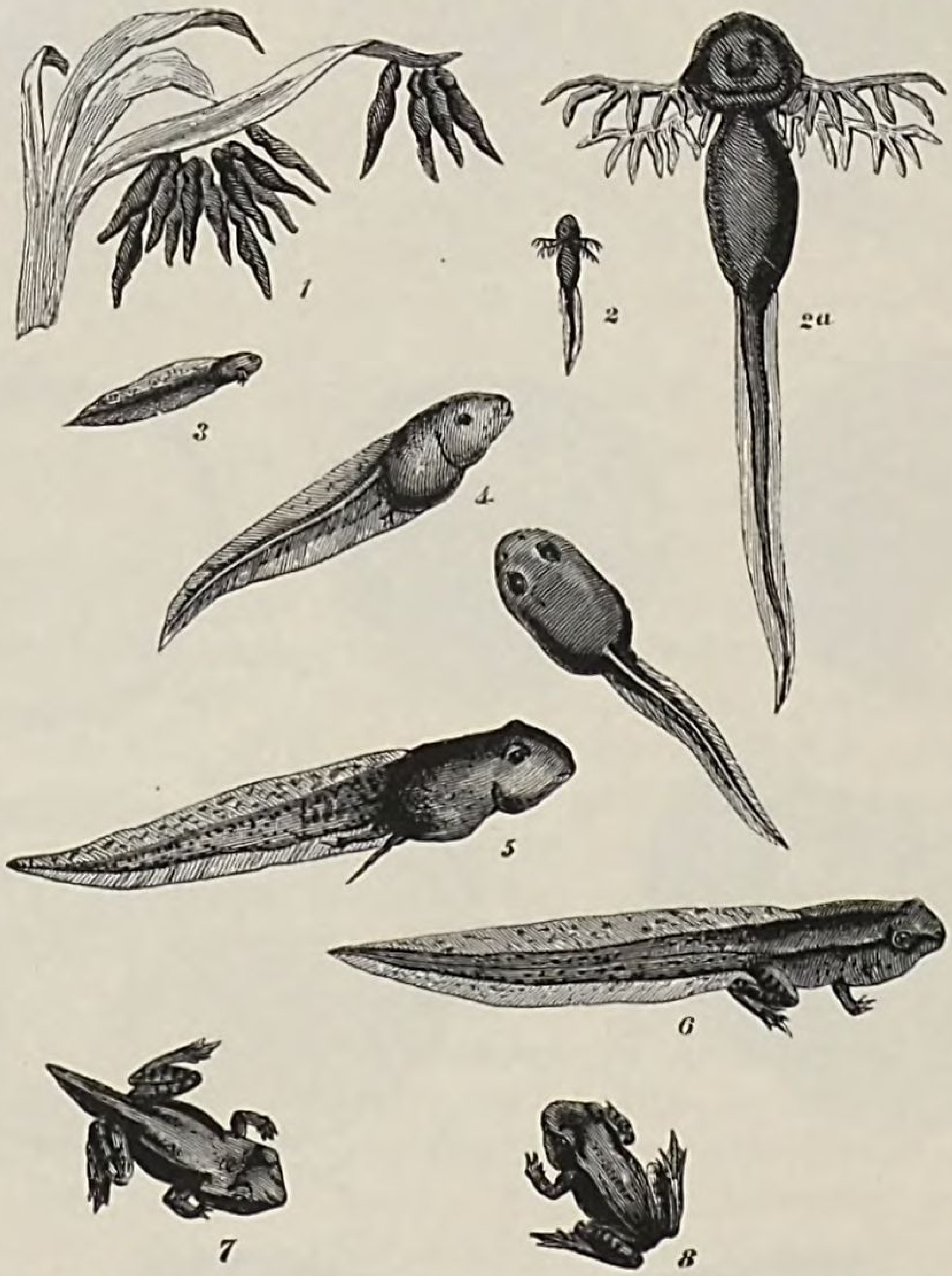


FIG. 886.—**Rana temporaria.** Stages in the life-history, from the newly-hatched Tadpoles (1) to the young Frog (8). 2^a is a magnified view of 2. (From Mivart.)

gills ($br^1.$, $br^2.$), and the regions from which they arise mark the positions of the first and second branchial arches.

The embryos are now hatched as *tadpoles.* They swim freely in the water or adhere to weeds by means of their suckers (Fig. 886, *1*). They are still blind and mouthless, the stomodæum not having yet communicated with the archenteron. Soon a third pair of external gills appears on the third branchial arch, and the first two pairs increase greatly in size (*2*, *2^a*); the stomodæum joins the archenteron, gill-slits are formed between the branchial arches,

and the eyes appear. The mouth is small, bounded by lips beset with horny papillæ and provided with a pair of horny jaws. The enteric canal grows to a great length and is coiled like a watch-spring, and the tadpole browses upon the water-weeds which form its staple food.

Soon the external gills show signs of shrivelling, and at the same time *internal gills*, like those of Fishes, are developed on the branchial arches. A fold of skin, the *operculum*, appears on each side, in front of the gills, growing from the region of the hyoid arch, and extends backwards until the gill-slits and external gills are covered, and there is only a single small external branchial aperture on each side, as in Holocephali (*3*, *4*). On the right side the operculum soon unites with the body-wall so as to close the branchial aperture, but on the left side the opening remains for a considerable time as the sole exit of the water. All this time the tadpole is to all intents and purposes a Fish.

The lungs now appear, and the larva is for a time truly amphibious, rising periodically to the surface to breathe air: the single branchial aperture, however, soon closes, and henceforth respiration is purely aërial.

In the meantime the limbs are developed. The hind-limbs appear as little rounded buds, one on each side of the root of the tail (*5*). The fore-limbs arise beneath the operculum and are therefore hidden at first; soon, however, they emerge by forcing their way through the operculum. As the limbs increase in size the tail undergoes a progressive shrinking (*6–8*). The mouth widens by the backward rotation of the suspensorium, the intestine undergoes a relative diminution in length, and vegetable is exchanged for animal diet. The little tailed Frog can now leave the water and hop about upon land; its tail is soon completely absorbed, and the metamorphosis is complete.

2. Distinctive Characters and Classification.

The Amphibia are Craniata which, in nearly all cases, possess gills either in the larval state only or throughout life, and which usually breathe by lungs in the adult condition. The skin is glandular, and there may or may not be a bony dermal exoskeleton. When unpaired fins are present they are never supported by fin-rays. The paired appendages, when present, are pentadactyle limbs: the digits are usually devoid of claws. The skull is autostylic and is articulated with the first vertebra by paired occipital condyles borne on the exoccipitals. The basi-occipital and supra-occipital are usually, and the basi-sphenoid is always, absent: there is a large parasphenoid and there are well-developed squamosals. In the branchiate forms large hyoid and branchial arches persist

throughout life: in the non-branchiate species these structures undergo more or less degeneration and give rise to the tongue-cartilage. The heart has a sinus venosus, right and left auricles, a single ventricle, and a conus arteriosus; the aortic arches arise from a bulbus aortæ or abbreviated ventral aorta. The cardinal veins undergo more or less degeneration and are practically replaced by an unpaired post-caval vein. There is a renal portal system, part of the returning blood from the posterior parts of the body going through it, the rest through the hepatic portal system by an abdominal vein which represents fused lateral veins. The red corpuscles are oval and nucleated and are often of unusual size. The lymphatic system is well developed. In the brain the small size of the cerebellum is noticeable. The olfactory sacs open into the mouth by posterior nares. The outer wall of the auditory capsule is pierced by a fenestra ovalis into which is inserted a cartilaginous stapes: the stapes may be connected by a columella with a tympanic membrane. The efferent ducts of the testis open into the urinary tubules, and the mesonephric duct of the male is a urinogenital duct. In the female the mesonephric ducts become the ureters, and the oviducts are pronephric ducts with cœlomic apertures. The pronephros is the functional kidney in the larva, the mesonephros in the adult. There is an allantoic bladder. Development is usually accompanied by a metamorphosis, the young being hatched in the form of a branchiate larva.

The Amphibia are classified as follows:—

Order 1. Urodela.

Amphibia which retain the tail throughout life. There are usually two pairs of limbs of approximately equal size.

The order is conveniently divided into—

a. *Perennibranchiata*, which retain the gills throughout life: including the American *Necturus*, the blind *Proteus* of the underground caves of Carniola in Dalmatia, and the Eel-like *Siren* of North America.

b. *Derotremata*, in which the gills are lost in the adult, but there is usually a persistent gill-cleft: including the Newt-like *Cryptobranchus* and the Eel-like *Amphiuma* from North America, and the Giant Salamander, *Megalobatrachus*, of China and Japan.

c. *Myctodera*, the Salamanders and Newts, in which the gills are lost and the gill-clefts closed in the adult: including the common Newts or Efts (*Molge*), the Spotted and Black Salamanders (*Salamandra*) of the European Continent, and the American *Amblystoma*, the sexually mature larva of which is the well-known *Axolotl*.

ORDER 2. ANURA.

Amphibia having no tail in the adult condition. The trunk is short and broad, and the hind-limbs greatly exceed the fore-limbs in size. Gills and gill-slits are never present in the adult.

Including the Frogs and Toads.

ORDER 3. GYMNOPHIONA.

Snake-like Amphibia having neither limbs nor tail. A dermal exoskeleton is present. There are no gills or gill-slits in the adult.

Including the Cæcilians (*Cæcilia*, *Epicrium*, &c.).

ORDER 4. STEGOCEPHALI.

Extinct tailed Amphibia, often of great size, having usually two pairs of limbs and a well-developed dermal exoskeleton. The group ranges from the Permian to the Trias.

Systematic Position of the Example.

The genus Rana belongs to the family *Ranidæ*, which with three other families constitutes the series *Firmisternia*, of the sub-order *Phaneroglossa*, and order *Anura*.

The absence of a tail and the presence of two pairs of limbs, of which the posterior are larger than the anterior, place the genus among the Anura. The presence of a tongue and of distinct paired Eustachian tubes separates the Phaneroglossa from the *Aglossa* (*Pipa* and *Xenopus*), a small group of Toads in which the tongue is absent and the Eustachian tubes have a common median opening. The Firmisternia are distinguished by having the coracoids joined by a common epicoracoid cartilage in contra-distinction from the *Arcifera* (Tree-frogs, Toads, &c.), in which the epicoracoids overlap one another. The Ranidæ are distinguished from the other families of Firmisternia by having teeth in the upper jaw and the transverse processes of the sacral vertebræ not dilated. R. temporaria is distinguished from R. esculenta by its smaller size and brown colour, by the large black patch in the tympanic region, and by the absence of external vocal sacs in the male.

3. GENERAL ORGANISATION.

The Amphibia are specially interesting as illustrating the transition from the water-breathing to the air-breathing type of Craniate structure. The lower forms retain their gills throughout life, but possess lungs in addition: in the higher the gills occur only in the larval state, and the adult breathes exclusively by the lungs and skin, becoming transformed from an aquatic into a

terrestrial animal. At the same time further adaptations to land-life take place, the most important being the modification of the blood-vessels consequent on the disappearance of the gills, the loss of median fins, and the strengthening of the limbs to support the weight of the body.

External Characters.—An excellent example of the lower Urodela with persistent gills is afforded by the great North American Water-newt, *Necturus maculatus* (Fig. 886 *bis*). The animal attains a length of 30 cm. (more than a foot); the elongated trunk is separated by a slight constriction from the depressed head and passes insensibly into the compressed tail, which is bordered by a continuous median fin unsupported by fin-rays. The limbs are small and weak in proportion to the size of the body, and in the ordinary swimming attitude are directed backwards, more or less parallel to the sagittal plane, the upper arm and thigh taking a direction backwards and slightly upwards, the fore-arm and hand and the shank and foot extending backwards and downwards. Each limb thus presents an external or dorsal and an internal or ventral surface, an anterior or *pre-axial* border which terminates in the first digit and a posterior or *post-axial* border which terminates in the last digit. The eyes are small and have no eyelids, there is no tympanic membrane, and the mouth is wide and bordered by thick lips. On each side of the neck are two gill-slits (*br. cl. 1*, *br. cl. 2*) leading into the pharynx, the first between the first and second branchial arches, the other between the second and third. From the dorsal end of each of the three branchial arches springs a branched *external gill* (*br. 1—br. 3*). Very similar in its external characters is the blind, cave-dwelling *Proteus*, and *Siren* (Fig. 887) differs mainly in its elongated eel-like body and in the absence of hind-limbs. All three genera are *perennibranchiate* or persistent-gilled.

The remaining Urodela are often called *caducibranchiate* or deciduous-gilled, and furnish a complete series of transitions from *derotrematous* forms which, while losing the gills, retain the gill-clefts, to *salamandrine* forms in which all trace of branchiate organisation disappears in the adult. In *Amphiuma* (Fig. 888) the body is eel-like and the limbs are extremely small: there are no gills in the adult, but two pairs of gill openings are retained throughout life. In *Cryptobranchus* there is a single branchial aperture, sometimes present on the left side only, but, as in the previously mentioned genera, four branchial arches are retained. In *Megalobatrachus*, the Giant Salamander of Japan and China, all trace of gill-slits disappears, but two branchial arches persist. Lastly, in the Salamanders, such as the Spotted Salamander (*Salamandra maculosa*, Fig. 889) of Europe and the common British Newts (*Molge*), the adult has no trace either of gills or gill-slits, and the branchial arches are much reduced. The limbs, also, in

the terrestrial Salamanders, stand out from the trunk, and have the soles of the feet and hands applied to the ground with the toes directed forwards, so as to support the weight of the body. More-



Fig. 886 *bis.*—**Necturus maculatus.** *an.* anus; *br.* 1–*br.* 3, external gills; *br. cl.* 1 and 2, branchial clefts.



Fig. 887.—**Siren lacertina.** (From Mivart.)



Fig. 888.—**Amphiuma tridactyla.** From Mivart.)

over, all trace of the median fin disappears, the tail becoming nearly cylindrical.

In the Anura the body is always Frog-like, the head being large and depressed, with a very wide mouth and large tympanic

membranes, the trunk short, the tail absent, and the hind- much larger than the fore-limbs. In the Toads, such as the common British *Bufo vulgaris*, and the tree-frogs (*Hyla*), the webs between the hind-toes are reduced or absent, and in many species of Hyla the toes end in rounded sucking-discs.

In the Gymnophiona (Fig. 890) the body is greatly elongated and snake-like, the head is small and not depressed, and the limbs are absent. There is no tail, the anus (*an.*) being at the posterior end of the body on the ventral surface. The Stegocephali, or Labyrinthodonts as they are frequently called, were mostly salamander-like,

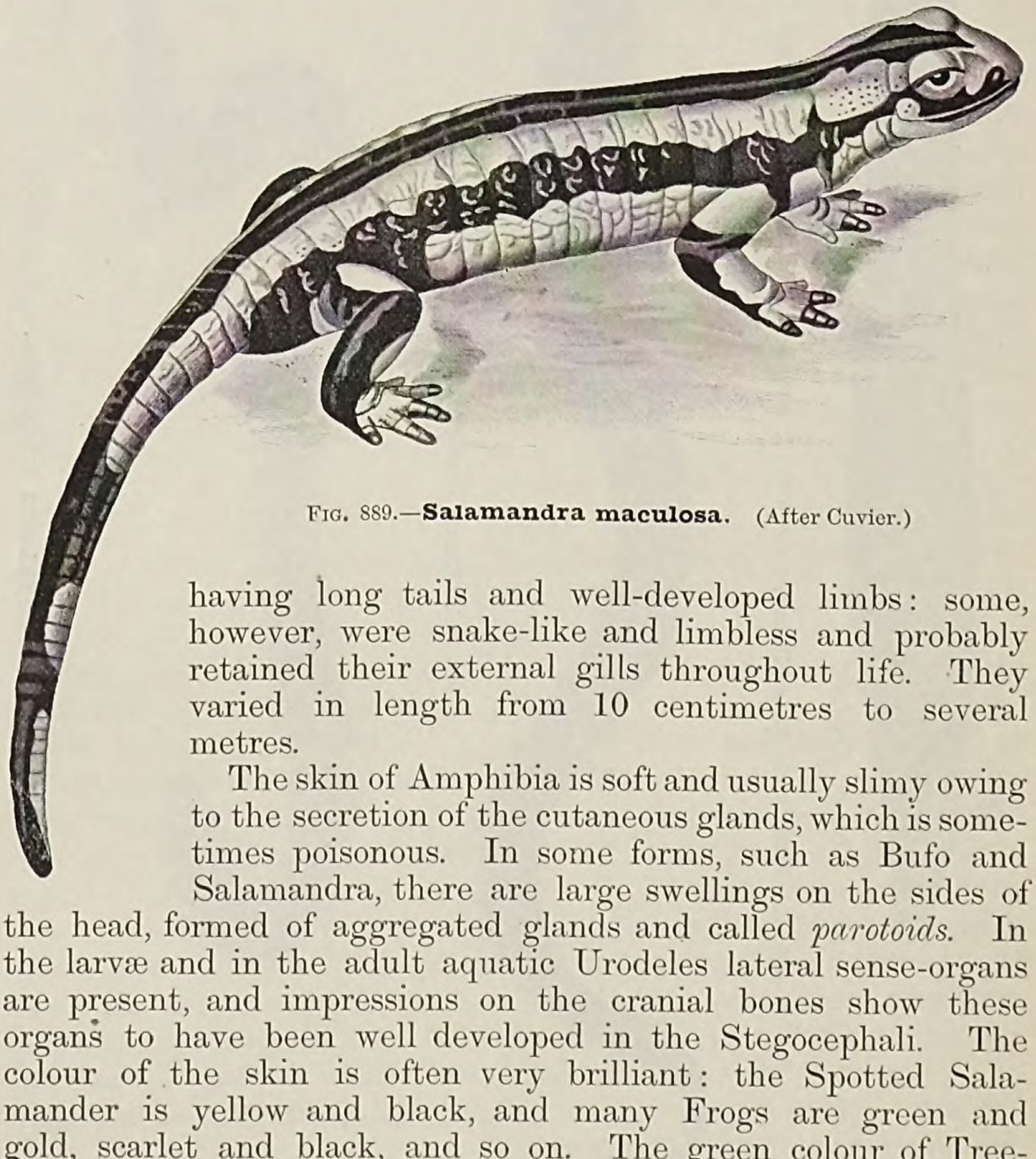


FIG. 889.—**Salamandra maculosa.** (After Cuvier.)

having long tails and well-developed limbs: some, however, were snake-like and limbless and probably retained their external gills throughout life. They varied in length from 10 centimetres to several metres.

The skin of Amphibia is soft and usually slimy owing to the secretion of the cutaneous glands, which is sometimes poisonous. In some forms, such as Bufo and Salamandra, there are large swellings on the sides of the head, formed of aggregated glands and called *parotoids*. In the larvæ and in the adult aquatic Urodeles lateral sense-organs are present, and impressions on the cranial bones show these organs to have been well developed in the Stegocephali. The colour of the skin is often very brilliant: the Spotted Salamander is yellow and black, and many Frogs are green and gold, scarlet and black, and so on. The green colour of Tree-frogs is protective, serving to conceal them among the foliage of the plants on which they live. The brilliant and strongly contrasted hues of the spotted Salamander and of some frogs are instances of "warning colours"; the animals are inedible

owing to the acrid secretion of their cutaneous glands, and their conspicuous colours serve to warn off the Birds and other animals which would otherwise devour them. A red and blue Nicaraguan Frog is said to show no sign of fear of the Frog-eating Birds, while the edible and more plainly coloured species are in constant danger. In many Toads the skin is dry and covered with warts.

An **exoskeleton** is present in many Gymnophiona in the form of small dermal scales, and in some Anura in the form of bony plates beneath the skin of the back. In the Stegocephali a very complete armour of bony scutes was present, sometimes covering the whole body, sometimes confined to the ventral surface. In a Urodele, *Onychodactylus*, and in the South African Toad, *Xenopus*, small pointed horny claws are present on the digits. With these exceptions the skin is devoid of hard parts.

Endoskeleton.—The *vertebral column* is usually divisible into a *cervical region*, containing a single vertebra devoid of transverse

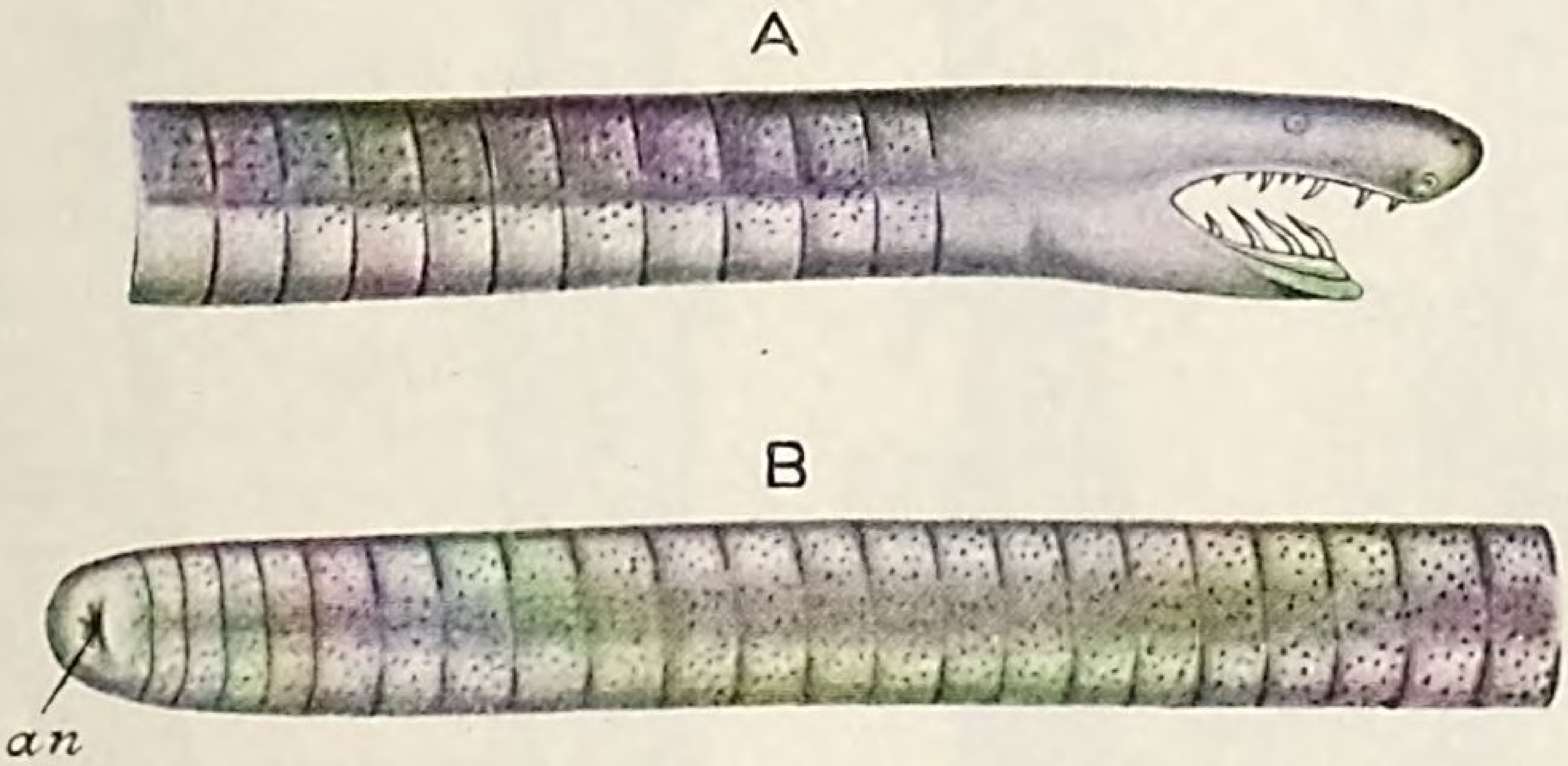


FIG. 890.—**Cœcilia pachynema.** A, anterior extremity from the right side; *B*, posterior extremity from beneath. *an*. anus. (After Boulenger.)

processes; an *abdominal* or *thoracico-lumbar region*, containing a variable number of vertebræ with transverse processes and often with ribs; a *sacral region*, containing a single vertebra, the large transverse processes, or the ribs, of which give attachment to the ilia; and a *caudal region*, forming the skeleton of the tail. In the Gymnophiona the caudal region is very short, and there is no sacrum: in the Anura the caudal region is represented by a single rod-shaped bone, the *urostyle*. The total number of vertebræ may reach 250 in Urodela and Gymnophiona: in Anura there are only nine vertebræ and a urostyle.

In the lower Urodela (Fig. 891, *A* and *B*) the centra are bi-concave as in Fishes: they consist of dice-box-shaped shells of bone, lined at either end by cartilage (*Jvk*), which is continuous between adjacent vertebræ. The bony shell is developed before the cartilage appears, so that the vertebræ are, in strictness, membrane bones. The neural arches, on the other hand, are far

more perfectly developed than in any Fish, and have well-formed zygapophyses, which articulate with one another by synovial joints.

The Gymnophiona also have biconcave vertebræ, but in the higher Urodela (Fig. 891, *C* and *D*) and the Anura absorption of cartilage takes place between adjacent centra in such a way that the convex

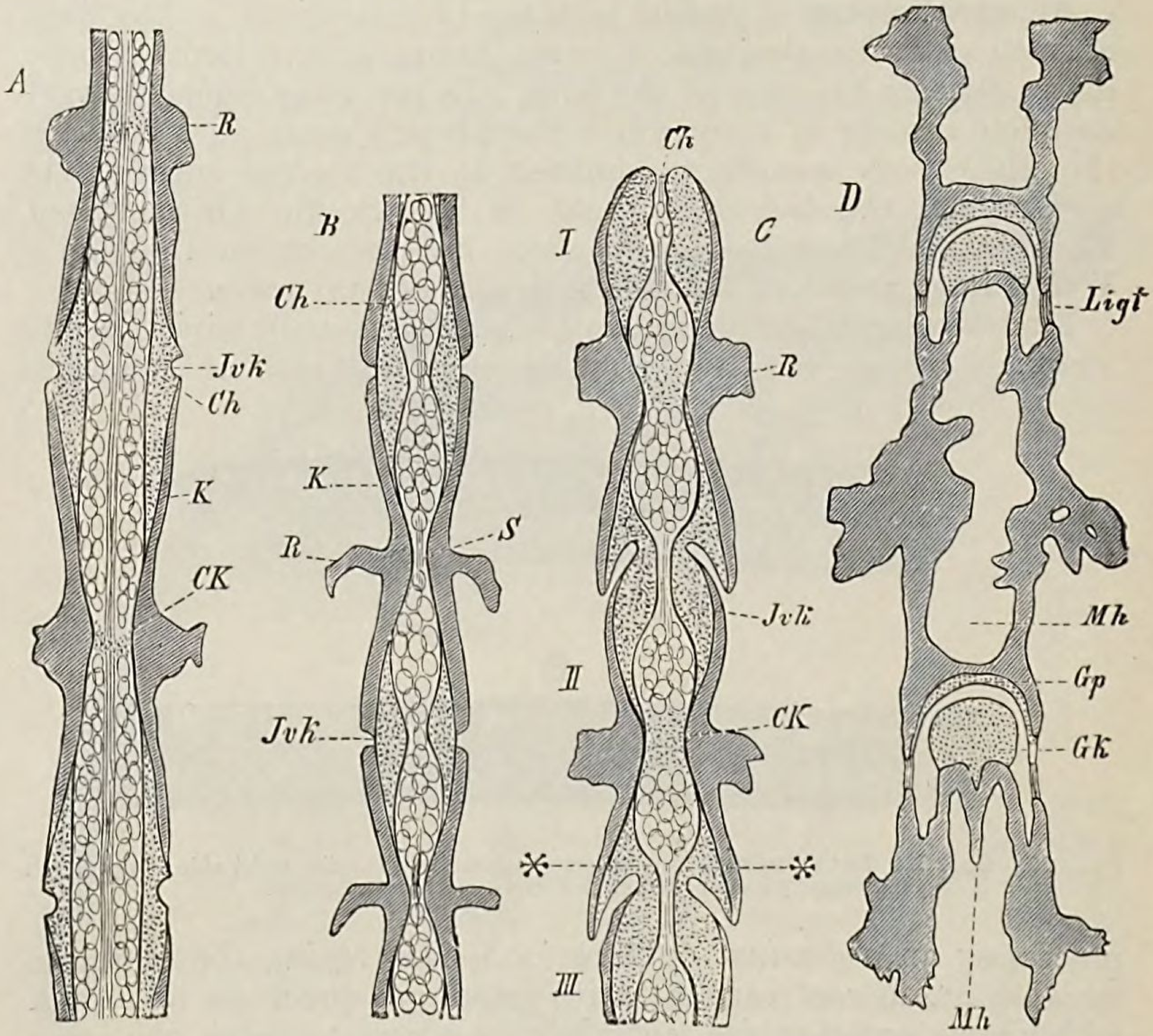


FIG. 891.—Longitudinal sections of vertebral centra of A, **Ranidens**; B, **Amblystoma**; C, **Spelerpes**; and D, **Salamandrina**. *Ch.* notochord; *CK*, intra-vertebral cartilage and fat-cells; *Gk*, convex anterior face of centrum; *Gp*, concave posterior face; *Jvk*, inter-vertebral cartilage; *K*, superficial bone of centrum; *Ligt.* inter-vertebral ligament; *Mh*, marrow-cavity; *R*, transverse process; *S* intra vertebral constriction. (From Wiedersheim's *Comparative Anatomy*.)

end of one fits into the concave end of the next, forming a cup-and-ball joint. In the higher Urodela the convexity is on the anterior, the concavity on the posterior face of each centrum (*D*), and the vertebræ are said to be *ophisthocœlous:* in the Anura they are usually, as in the Frog, procœlous. In the Stegocephali there is great diversity in the structure of the vertebral column. There may be well-developed dice-box-shaped centra, or the neural arches may be simply

perched upon a persistent notochord surrounded by incomplete hoops of bone, twice as numerous as the arches, and alternately dorsal and ventral in position. The former represent centra, the latter *inter-centra* or ossifications alternating with the centra on the ventral region of the notochord.

The first or cervical vertebra bears paired articular surfaces for the condyles of the skull, and between them the anterior face of the centrum gives off, in Urodela, a projection called the *odontoid process.* The Urodela, moreover, have *ribs* articulating with the transverse processes of the abdominal and sacral vertebræ: they are short bones, forked proximally, and the compressed transverse processes are correspondingly divided. The sacral ribs of Urodeles give attachment to the ilia, and the caudal vertebræ bear hæmal arches.

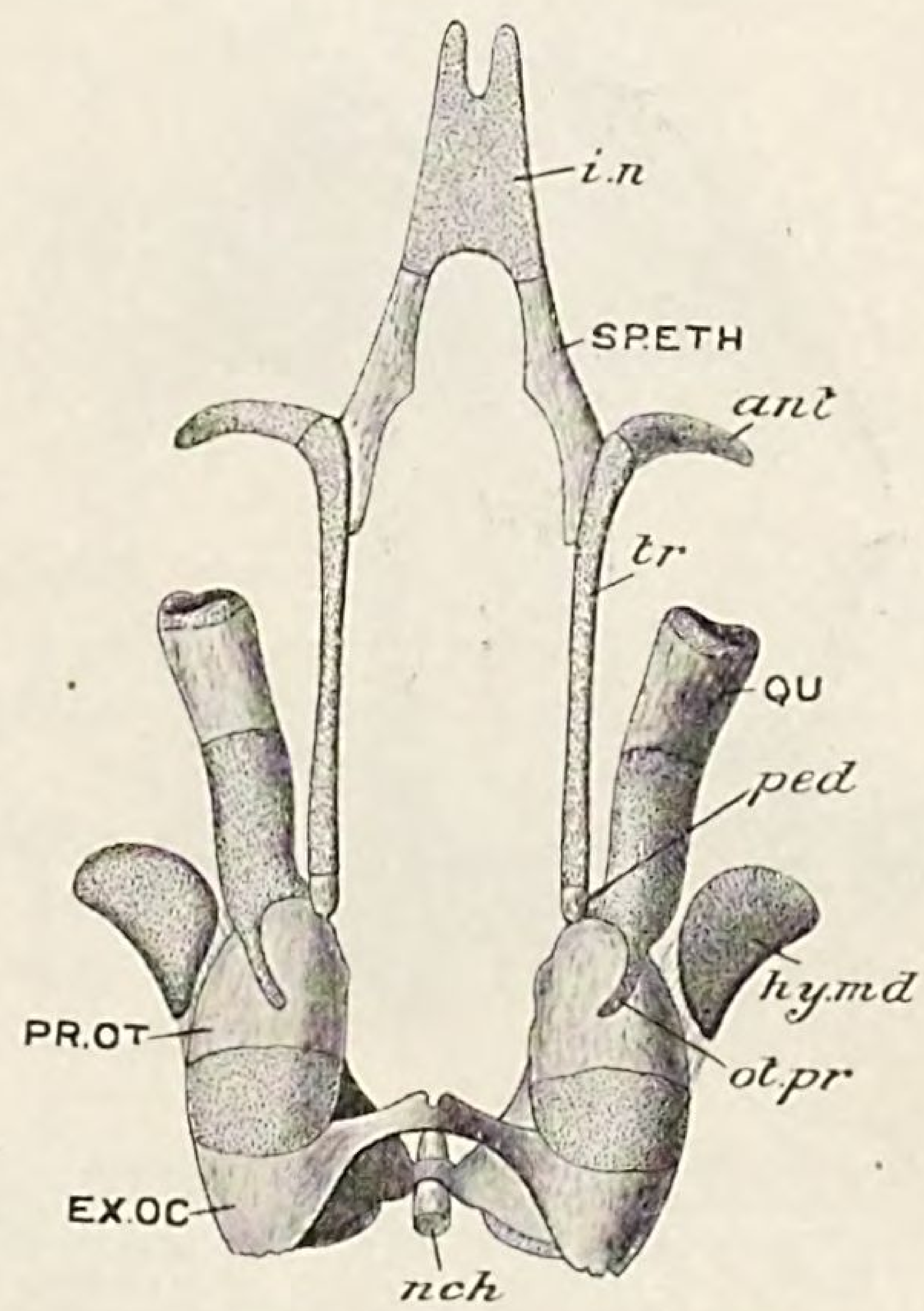


FIG. 892.—**Proteus anguinus.** The chondrocranium from above. *ant.* antorbital process; **EX.OC.** exoccipital and epiotic; *hy.md.* hyomandibular; *i.n.* inter-nasal plate; *nch.* notochord; *ot. pr.* otic process; *ped.* pedicle; **PR.OT.** prootic; **QU.** quadrate; **SP.ETH.** sphenethmoid. (After W. K. Parker.)

The *skull* of Urodela differs from that of the Frog in many important respects, the most striking of which is the fact that the trabeculæ do not meet either below the brain to form a basis cranii or above it to form a cranial roof. Thus when the membrane bones are removed the cranium (Fig. 892) is completed above and below in the parachordal or occipital region only: anterior to this it has side walls, but no roof or floor, there being above a huge superior cranial fontanelle, and below an equally large basi-cranial fontanelle, the former covered, in the entire skull, by the parietals and frontals, the latter by the parasphenoid. In the perennibranchiate forms Necturus and Proteus the trabeculæ remain, even in the adult, as narrow cartilaginous bars, and the chondrocranium is actually of a lower or more embryonic type than that of any other Craniate, with the possible exception of Cyclostomata.

In the Urodela, moreover, the parietals (Fig. 893, *P*) and frontals (*F*) are separate, the parasphenoid (*Ps*) is not T-shaped, the palatine and pterygoid are sometimes represented by a single bone

(*Pt*), and the palatine, when distinct, bears teeth. The suspensorium is inclined forwards, as in the Tadpole, not backwards as in the adult Frog. The hyoid arch is large, and its dorsal end may be separated as a hyomandibular. There are three or four branchial arches which are large in the perennibranchiate forms, but undergo more or less reduction in caducibranch species, never, however, forming such a simple tongue-bone as that of the Frog. The stapes has no columella attached to it, and in correspondence with this there is no tympanic cavity or membrane

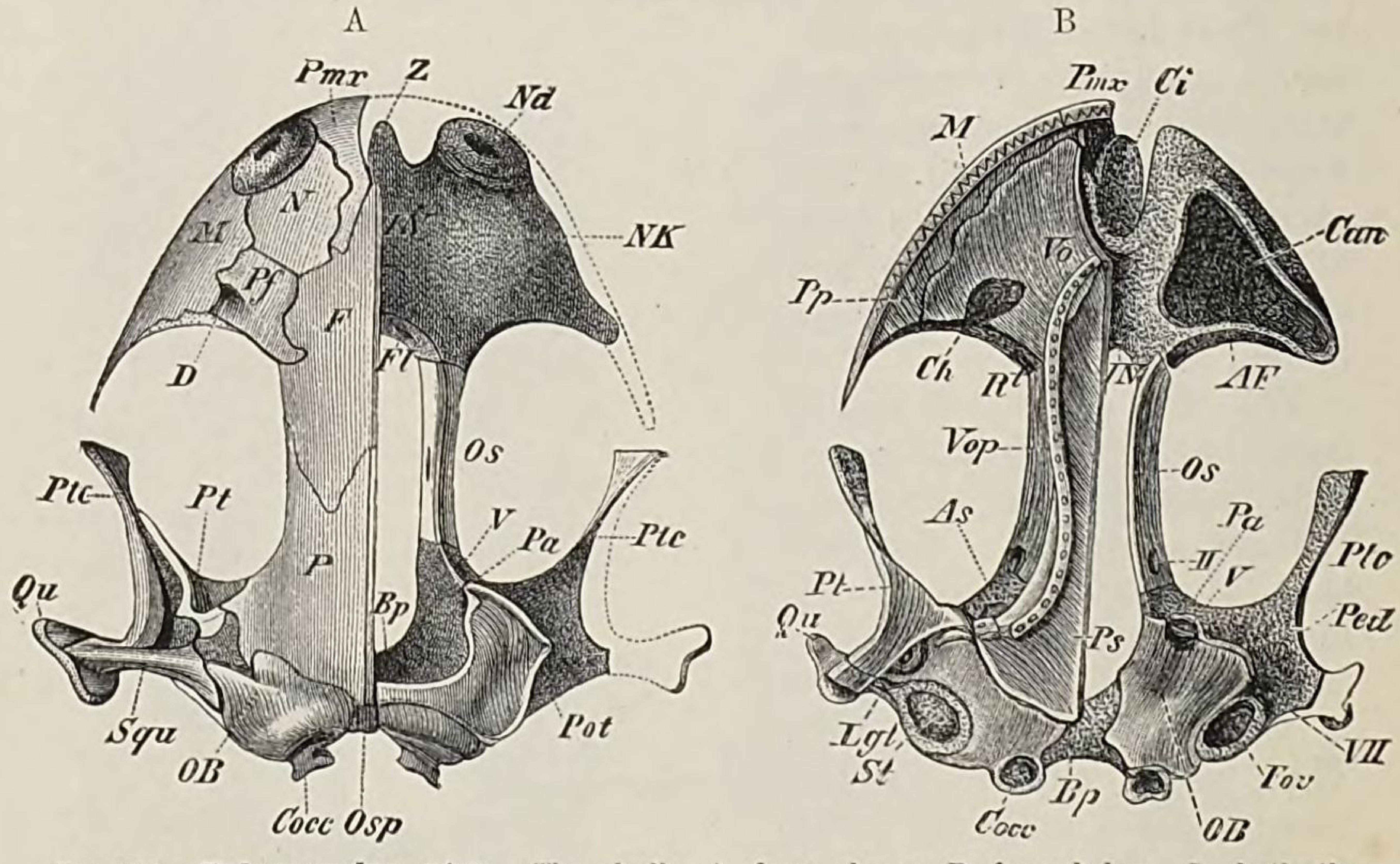


Fig. 893.—**Salamandra atra.** The skull. A, from above; B, from below. In both the membrane bones are removed on the right side of the figure. *Af*, antorbital process; *As*, alisphenoid; *Bp*, basal plate; *Can*, nasal cavity; *Ch*, posterior nares; *Ci*, process of internasal plate; *Cocc.* occipital condyles; *D.* aperture of lacrymal duct; *F.* frontal; *Fl*, olfactory foramen; *Fov.* fenestra ovalis; *IN.* internasal plate; *Lgt.* ligament connecting stapes with suspensorium; *M.* maxilla; *N.* nasal; *Na.* nasal aperture; *NK*, olfactory capsule; *OB*, auditory capsule; *OS*, sphenethmoid; *Osp*, supra-occipital region; *P*, parietal; *Pa*, ascending process of suspensorium; *ped.* pedicle; *Pf.* pre-frontal; *Pmx.* pre-maxilla; *Pot.* otic process of suspensorium; *Pp.* palatine process of maxilla; *Ps.* parasphenoid; *Pt.* pterygoid bones; *Ptc.* pterygoid cartilage; *Rt*, foramen for nasal branch of trigeminal; *Qu.* quadrate; *Squ.* squamosal; *St.* stapes; *Vo.* vomer; *Vop.* vomero-palatine; *Z*, process of internasal plate; *V*, trigeminal foramen; *VII*, facial foramen. (From Wiedersheim's *Comparative Anatomy*.)

In the Anura there is a very wide range of variation in the skull. Among the most important points are the presence, in a few species, of small supra- and basi-occipitals, and the fact that in others the roofing membrane-bones are curiously sculptured and so strongly developed as to give the skull a singularly robust appearance.

In the Gymnophiona (Fig. 894) very little of the original cartilage remains in the adult state, but the membrane bones are very large and form an extremely complete and substantial structure, especially remarkable for the way in which the small

orbit (*Orb.*) is completely surrounded by bones. In the Stegocephali (Fig. 895) the skull is broad and flattened, the supra-occipital (*s. occ.*) double, and the parietals (*P*) and frontals (*F*) are separate. Between the parietals is an aperture, the *parietal foramen* (*Fp*), which perhaps lodged a pineal eye. The eyes were sometimes surrounded by a ring of bony *sclerotic plates* (*Oc.*). Gill-arches have been found in many species.

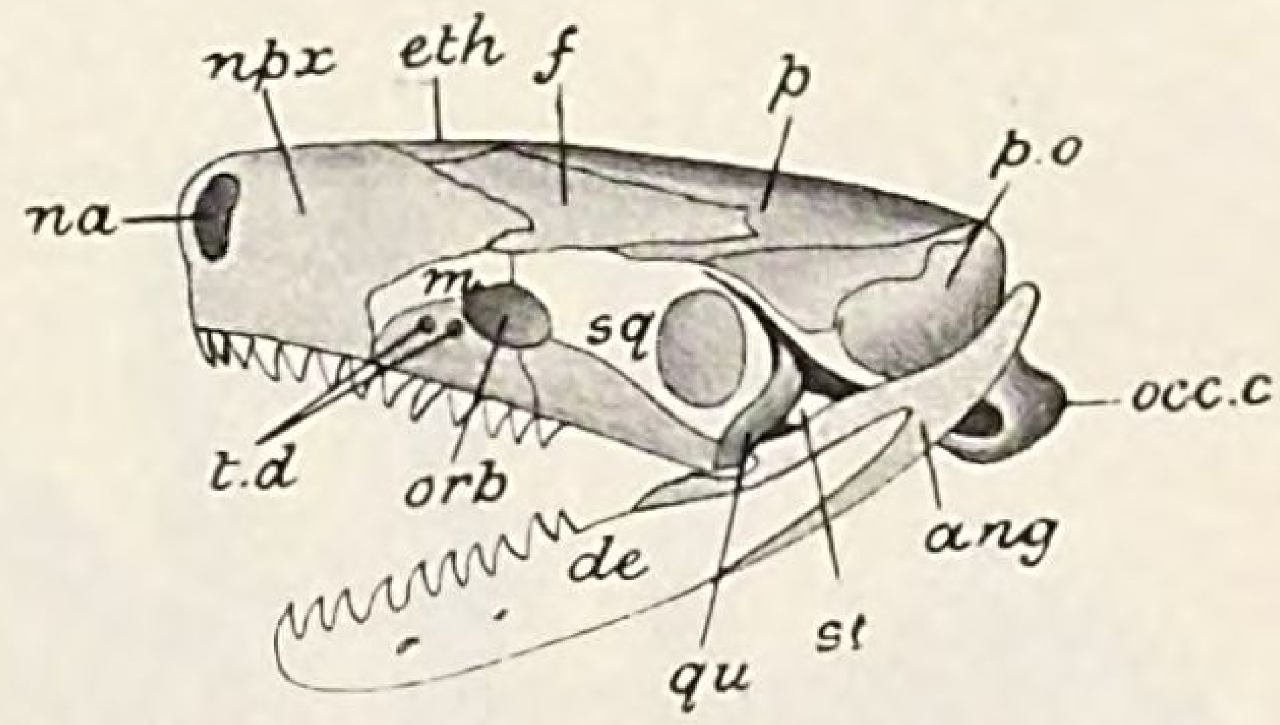


FIG. 894.—Skull of **Siphonops annulatus.** *Ang.* angular; *occ.c.* occipital condyle; *de.* dentary; *eth.* ethmoid; *f.* frontal; *m.* maxilla; *na.* nasal aperture; *npx.* naso-premaxilla; *orb.* orbit; *p.* parietal; *p.o.* ex-occipital and otic bones; *qu.* quadrate; *sq.* squamosal; *t.d.* ducts of tentacle glands. (From Wiedersheim.)

The *shoulder-girdle* of Urodela (Fig. 896) is chiefly remarkable for the great size of the unossified coracoids (A. *Co.*, B. *C.*) which overlap one another on the ventral body-wall. The procoracoid (*Cl*) is also large, and there is no clavicle. The *sternum* (*St*) is usually a more or less rhomboid plate of cartilage between the posterior ends of the coracoids, and there is no omosternum. In Necturus, however, the sternum presents a very interesting structure: it is a narrow, irregular, median bar, sending off branches right and left into the myocommas, a condition of things which suggests its origin by the fusion of *abdominal ribs* or supporting structures developed between the ventral portions of the myomeres, just as the true ribs are formed between their dorsal portions. In the Anura the epicoracoids either simply meet one another in the middle ventral line, as in Rana, or overlap, as in the Fire-toad (*Bombinator*) and the Tree-frogs (*Hyla*). The overlapping of the coracoids, in Anura as in Urodela, is sometimes correlated with the absence of an omosternum. In the Stegocephali there is a median ventral membrane-bone, the *inter-clavicle*, which is connected on each side with the clavicle, and extends backwards ventral to the sternum. There is also, on each side, a bone called the *cleithrum*, connected with

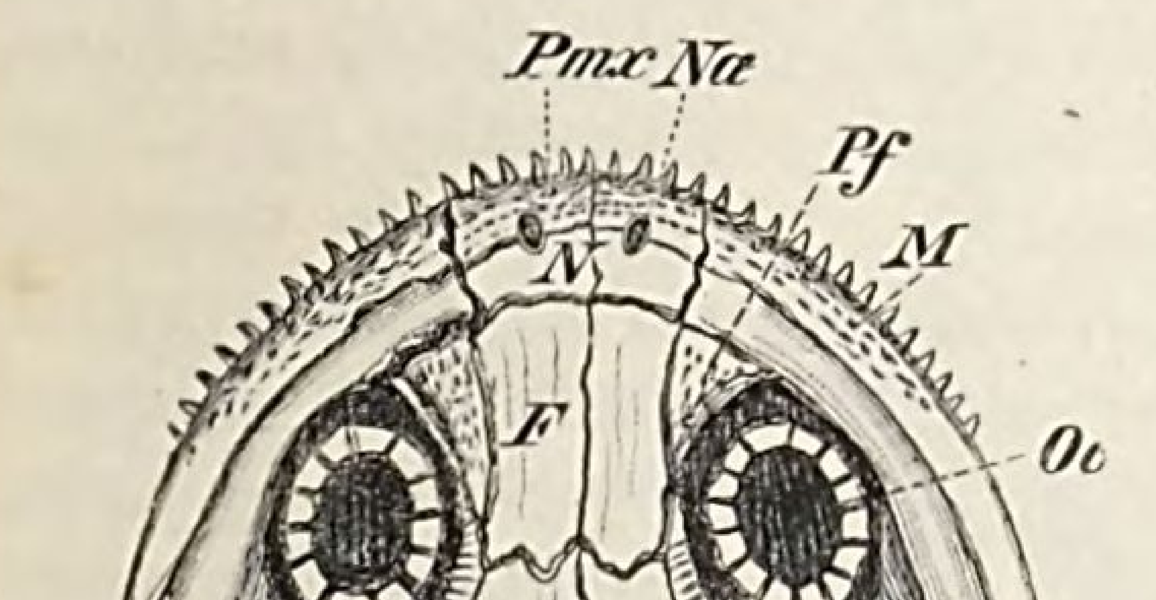


FIG. 895.—Skull of **Protriton,** one of the smaller Stegocephali, magnified. *Br.* branchial arches; *F.* frontal; *Ff,* parietal foramen; *M.* maxilla; *N.* nasal; *Na.* nostril; *Oc,* sclerotic plates; *P.* parietal; *Pf.* pre-frontal; *Pmx.* pre-maxilla; *Socc.* supra-occipital. (From Wiedersheim.)

the corresponding clavicle: there is some reason for thinking it to be homologous with the bone usually called clavicle in Teleostomi.

In the *pelvic girdle* of the Urodela the combined pubic and ischiatic regions (Fig. 897, *P*, *Is*) of the right and left sides are united to form an elongated cartilaginous plate which gives off on each side, above the acetabulum (*G*), a slender vertical rod, the ilium (*Il*[1]). Ossifications are formed in the iliac and ischiatic regions, but the pubic region remains cartilaginous. The resemblance of the pelvis of the lower Urodela, and especially of Necturus, to those of Polypterus (p. 216) and of the Dipnoi (p. 233) is noteworthy. In Anura the pelvic girdle resembles that of the Frog.

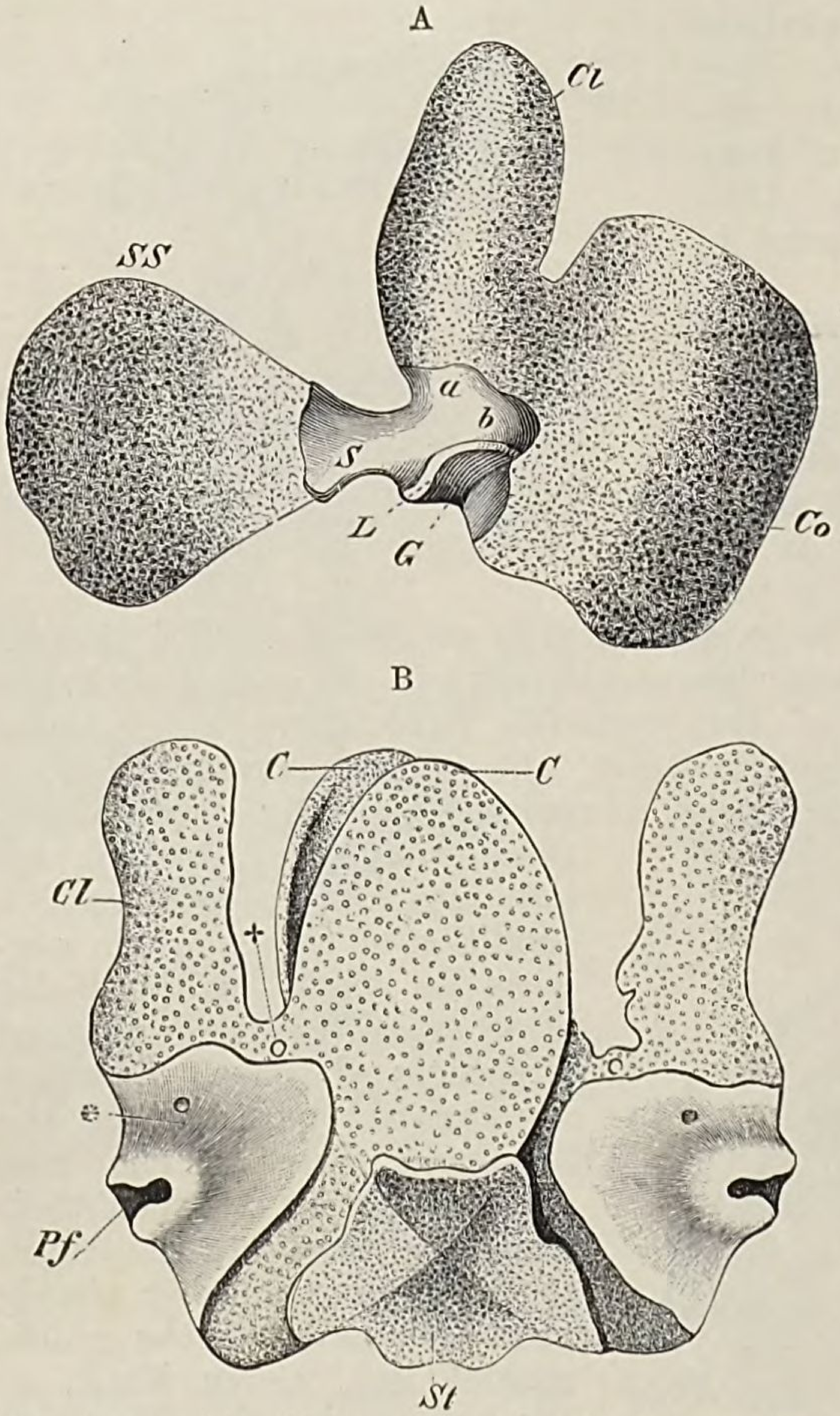


FIG. 896.—A, right side of shoulder-girdle of **Salamandra**; B, shoulder-girdle and sternum of **Amblystoma** (Axolotl) from the ventral aspect. *a*, *b*, processes of scapula; C (in B), coracoid; *Cl.* pro-coracoid; *Co.* (in A), coracoid; *G.* (in A), glenoid cavity; *L*, its cartilaginous edge; *Pf* (in A), glenoid cavity; *s.* scapula; *SS.* supra-scapula; *st.* sternum; *, †, nerve foramina. (From Wiedersheim.)

Attached to the anterior border of the pubic region there occurs in many Urodela and in Xenopus, a rod of cartilage, forked in front, the *epipubis* (*Ep*). It is developed independently of the pelvis, and its relations to that structure are very similar to those of the sternum to the shoulder-girdle; it has, in fact, been proposed to call it a *pelvi-sternum*.

The limbs of Urodela differ from the typical structure already described only in details: there are usually four digits in the fore-limb and five in the hind-limb. In Anura the limbs are modified by the fusion of the radius and ulna and of the tibia and fibula, and by the great elongation of the two proximal tarsals. A pre-hallux is frequently present.

Myology.—In the lower Urodela the muscles of the trunk and tail occur in the form of typical myomeres like those of Fishes. In the higher forms the myomeres become converted into longitudinal dorsal bands, the *extensors of the back*, paired ventral bands, the *recti abdominis*, and a double layer of *oblique* muscles, covering the flanks.

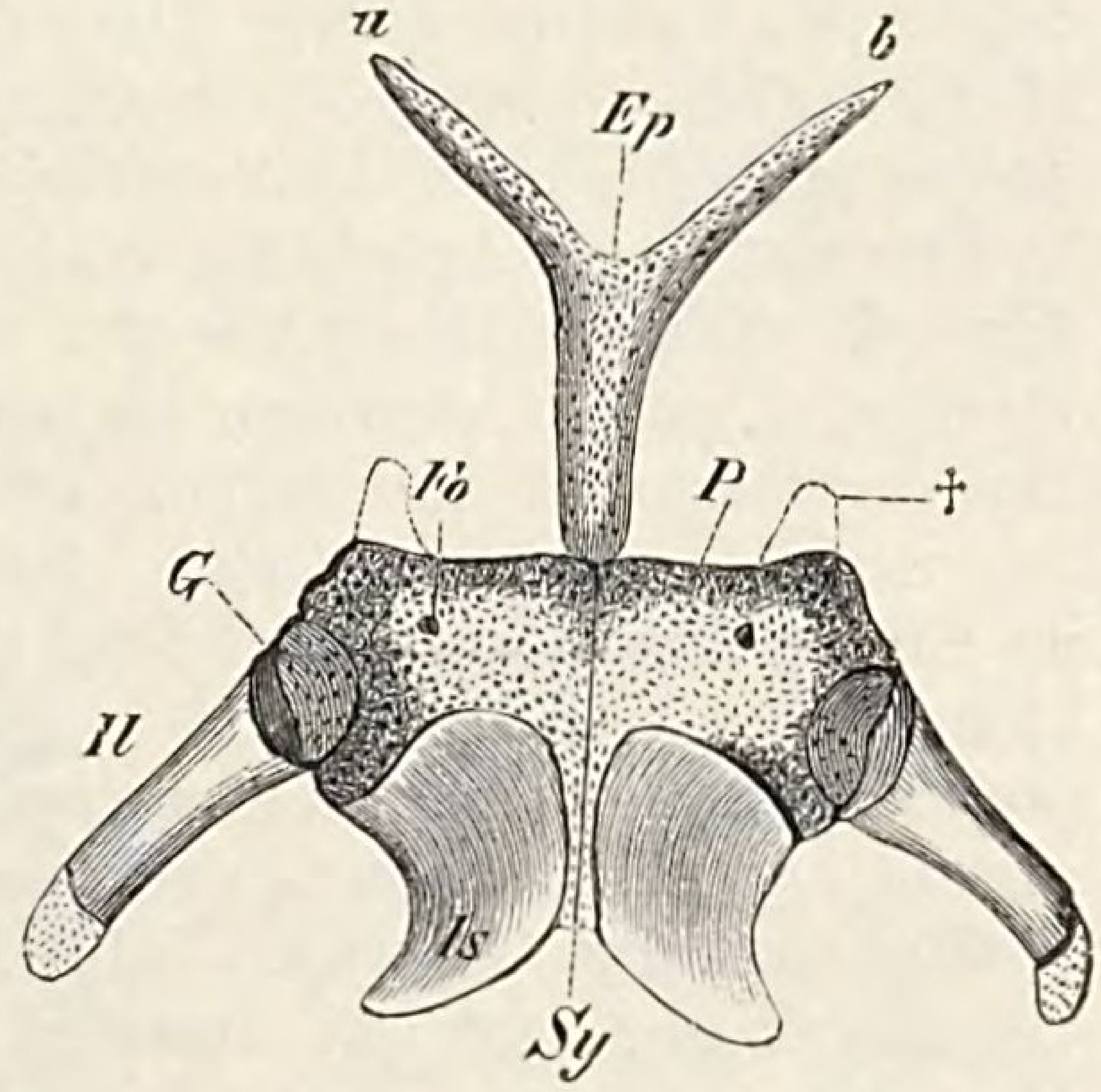


FIG. 897.—Pelvic girdle of **Salamandra.** *A, b,* processes of epipubis; *Ep.* epipubis; *Fo.* obturator foramen; *G.* acetabulum; *Il.* ilium; *Is.* ischium; *P.* pubis; *Sy.* pubo-ischiatic symphysis; †. processes of pubis present in some Urodeles. (From Wiedersheim.)

Digestive Organs.—The *teeth* are always small and ankylosed to the bones: they may be singly or doubly pointed. They occur most commonly on the premaxillæ, maxillæ, and vomers, but may also be developed on the dentaries, palatines, and, in one instance, on the parasphenoid. In many Anura, such as the Common Toad, teeth are altogether absent. In some of the Stegocephali, such as *Mastodonsaurus*, the teeth are extraordinarily complex in structure, the tissues being folded in such a way as to produce in section a complex tree-like pattern. It is from this circumstance that the term *Labyrinthodont*, often applied to the Stegocephali, is derived.

The *enteric canal* is divisible into buccal cavity, pharynx, gullet, stomach, small intestine, rectum, and cloaca. The stomach and duodenum together form a U-shaped loop in which the pancreas lies. The *tongue* in many Urodeles is fixed and immovable, like that of a Fish: in most Anura it is free behind, as in the Frog, but in Xenopus and Pipa (hence called *Aglossa*) it is absent.

Respiratory Organs.—With very few exceptions Amphibia possess *external gills* in the larval state, and, in the perennibranchiate Urodela, these organs are retained throughout life. They are branched structures, abundantly supplied with blood, and springing from the dorsal ends of the first three branchial arches. The epithelium covering them is ectodermal, so that they are cutaneous and not pharyngeal gills, and are of a totally different

nature from the so-called external gills of the embryos of Elasmobranchs and Holocephali, which are only the filaments of the internal gills prolonged through the branchial apertures.

Internal gills are developed only in the larvæ of Anura. They appear as papillæ on the outer borders of the branchial arches below the external gills. They closely resemble the internal gills of Fishes and appear to be homologous with them, although it seems probable that their epithelium is ectodermal.

In most adult Amphibia *lungs* are formed as outgrowths of the ventral wall of the pharynx. The right and left lungs communicate with a common *laryngo-tracheal chamber*, supported by the cartilages of the larynx and opening into the mouth by a longitudinal slit, the *glottis*. In the more elongated forms, such as Siren, Amphiuma, and the Gymnophiona, the laryngo-tracheal chamber is prolonged into a distinct *trachea* or wind-pipe, supported by cartilages. In many species of Salamanders the lungs are absent and respiration is exclusively cutaneous and pharyngeal.

Circulatory Organs.—The *heart* always consists of a sinus venosus, right and left auricles, ventricle, and conus arteriosus. The sinus venosus opens into the right auricle, the pulmonary veins enter the left, and the two are separated by a septum auricularum which forms a complete partition in Anura, but in Urodela and Gymnophiona is more or less fenestrated, *i.e.* formed of a network of muscular strands with intervening spaces. The conus arteriosus has no longitudinal valve in the lower Urodela and the Gymnophiona, but is separated both from the ventricle and from the bulbus aortæ by transverse rows of valves.

In the perennibranchiate Urodela and in the larvæ of the air-breathing forms the circulation is essentially like that of a Fish. The bulbus aortæ (Fig. 898, A, *b. ao.*), which represents an abbreviated ventral aorta, gives off four *afferent branchial arteries* (*af. br. a.* 1—4), three to the external gills, and a fourth which curves round the gullet and joins the dorsal aorta directly. From each gill an *efferent branchial artery* brings back the purified blood, and the efferent arteries unite, in a somewhat irregular way, to form the dorsal aorta (*d. ao.*). Each afferent with the corresponding efferent artery constitutes an *aortic arch*. Short connecting branches unite the afferent and efferent arteries of each gill, carotids (*ext. car.*, *int. car.*) are given off from the first efferent artery, and, when the lungs appear, a *pulmonary artery* (*pul. a.*) is given off from the dorsal portion of the fourth aortic arch of each side. When the gills atrophy (B) the first aortic arch loses its connection with the dorsal aorta and becomes the carotid trunk; the second increases in size, forming the main factor of the dorsal aorta, and becomes the systemic trunk; the third undergoes great reduction, and the fourth becomes the pulmonary artery, its dorsal portion retaining its connection with

the systemic trunk in the form of a small connecting branch, the *ductus Botalli* (*d. bot.*). In the Anura, as we have seen (p. 261), the third arch vanishes completely and there is no ductus Botalli.

As to the *venous system*, the Urodela exhibit very clearly the transition from the Fish-type to the condition already described in the Frog. The blood from the tail is brought back by a *caudal vein* (Fig. 899, *Caud. v.*) which, on reaching the cœlome, divides into two *renal portal veins*, one going to each kidney. From the kidney the blood is taken, in the larva, into paired *cardinal veins*, each of which joins with the corresponding *jugular* to form a *precaval vein*.

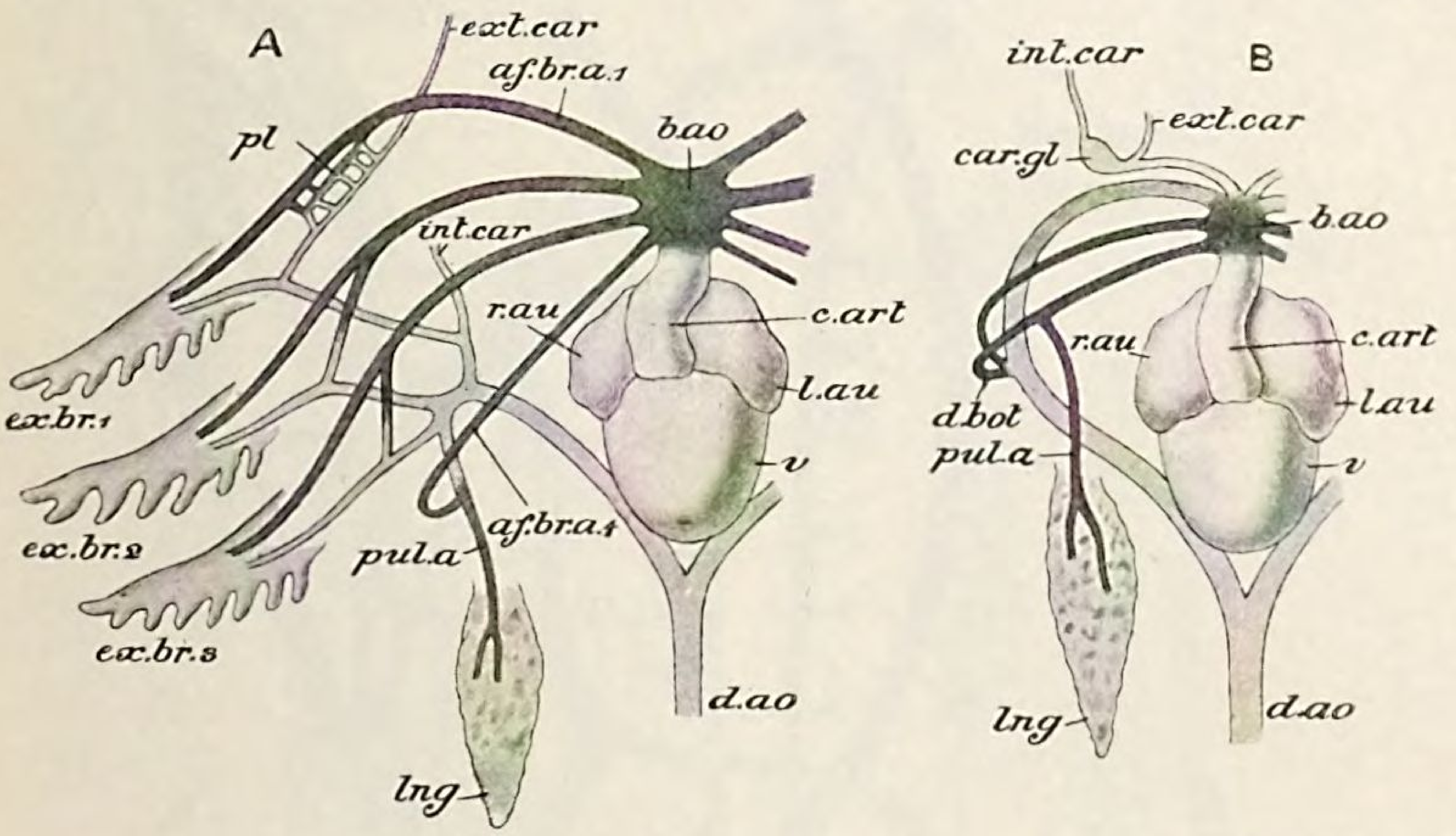


FIG. 898.—Heart and chief arteries of **Salamandra.** A, larva; B, adult. *af. br. a.* 1—4, afferent branchial arteries; *b. ao.* bulbus aortæ; *car. gl.* carotid gland; *c. art.* conus arteriosus; *d. ao.* dorsal aorta; *d. bot.* ductus Botalli; *ex. br.* 1—3, external gills; *ext. car.* external carotid; *int. car.* internal carotid; *l. au.* left auricle; *lng.* lung; *pl.* plexus, giving rise to carotid gland; *pul. a.* pulmonary artery; *r. au.* right auricle; *v.* ventricle. (Altered from Boas.)

In the adult the anterior portions of the cardinals undergo partial atrophy, becoming reduced to two small *azygos veins* (*card. post.*) which receive the blood from the region of the back: their posterior portions unite and are continued forwards by a new unpaired vein, the *post-caval* (*V. cava. inf.*), which, joined by the hepatic veins, pours its blood into the sinus venosus. The iliac vein from the hind-leg divides into two branches: one joins the renal portal, the other, representing the lateral vein of Elasmobranchs, unites with its fellow in the middle ventral line to form the *abdominal vein* (*Abd. V.*) and joins the hepatic portal, whence its blood, after traversing the capillaries of the liver, is returned by the hepatic vein into the post-caval.

The red corpuscles are oval and nucleated, and are remarkable for their unusual size. Those of Amphiuma are the largest

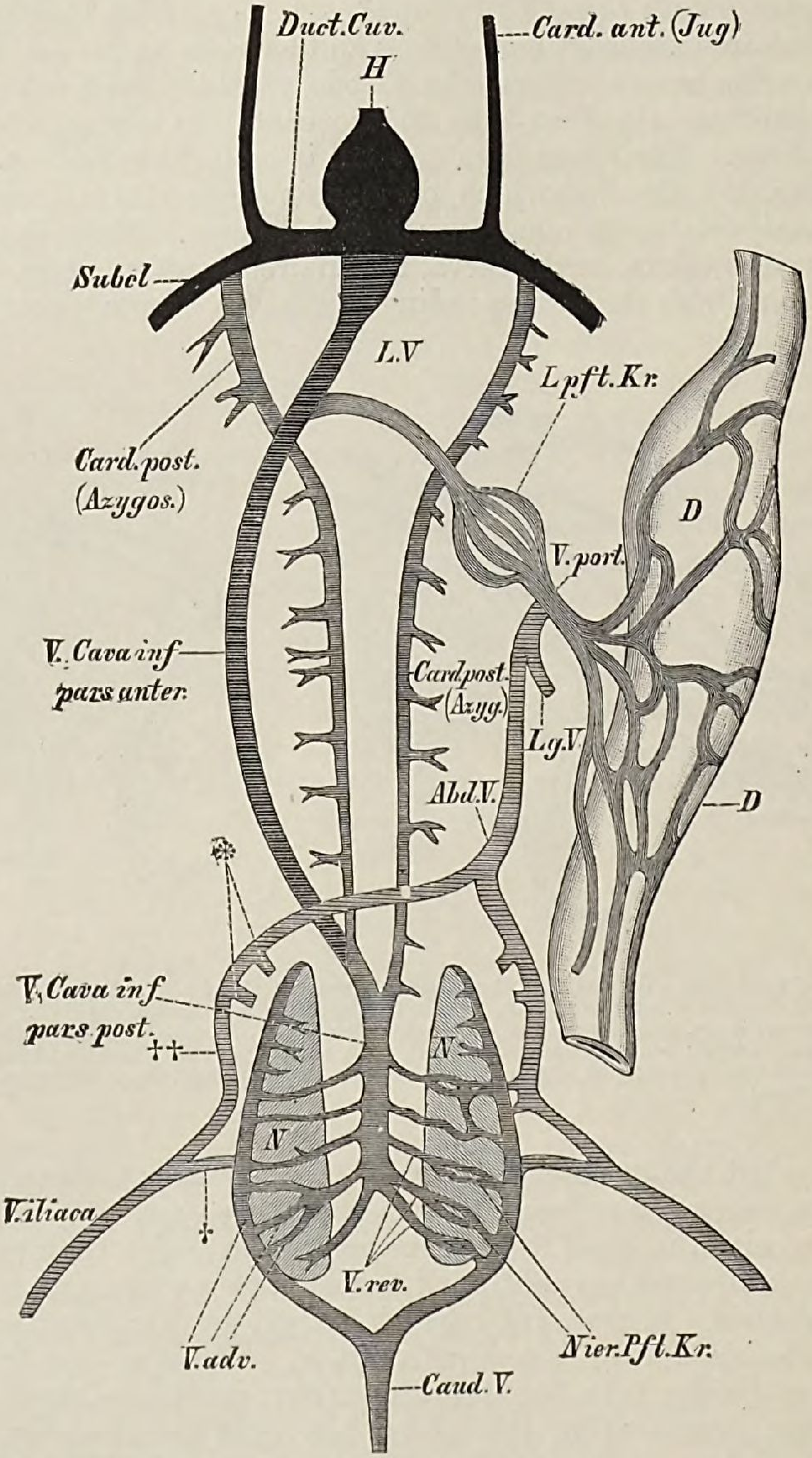


FIG. 899.—**Salamandra maculosa.** Venous system, diagrammatic, from the ventral aspect. *Abd. v.* abdominal vein; *Card. ant.* (*Jug.*), jugular vein; *card. post.* (*azyg.*), azygos vein; *Caud. V.* caudal vein; *D*, intestine; *Duct. Cuv.* precaval vein; *H.* heart; *Lg. V.* mesenteric vein; *L. pft. Kr.* hepatic portal system; *LV.* hepatic vein; *N*, kidney; *Nier. Pft. Kr.* renal portal system; *Subcl.* subclavian vein; *V. adv*, branches of renal portal vein; *V. cava. inf.* post-caval; *V. iliaca*, iliac vein; *V.*, *rev.* renal veins; *, cloacal veins; †, branch of iliac to renal portal vein; † †, lateral vein. (From Wiedersheim.)

known, being about $\frac{1}{14}$ mm. in diameter, or eight times that of a human red corpuscle.

Nervous System and **Sense Organs.**—The *brain* of Urodela differs from that of the Frog in its more elongated and slender form, in the comparatively small size of the optic lobes, and in the

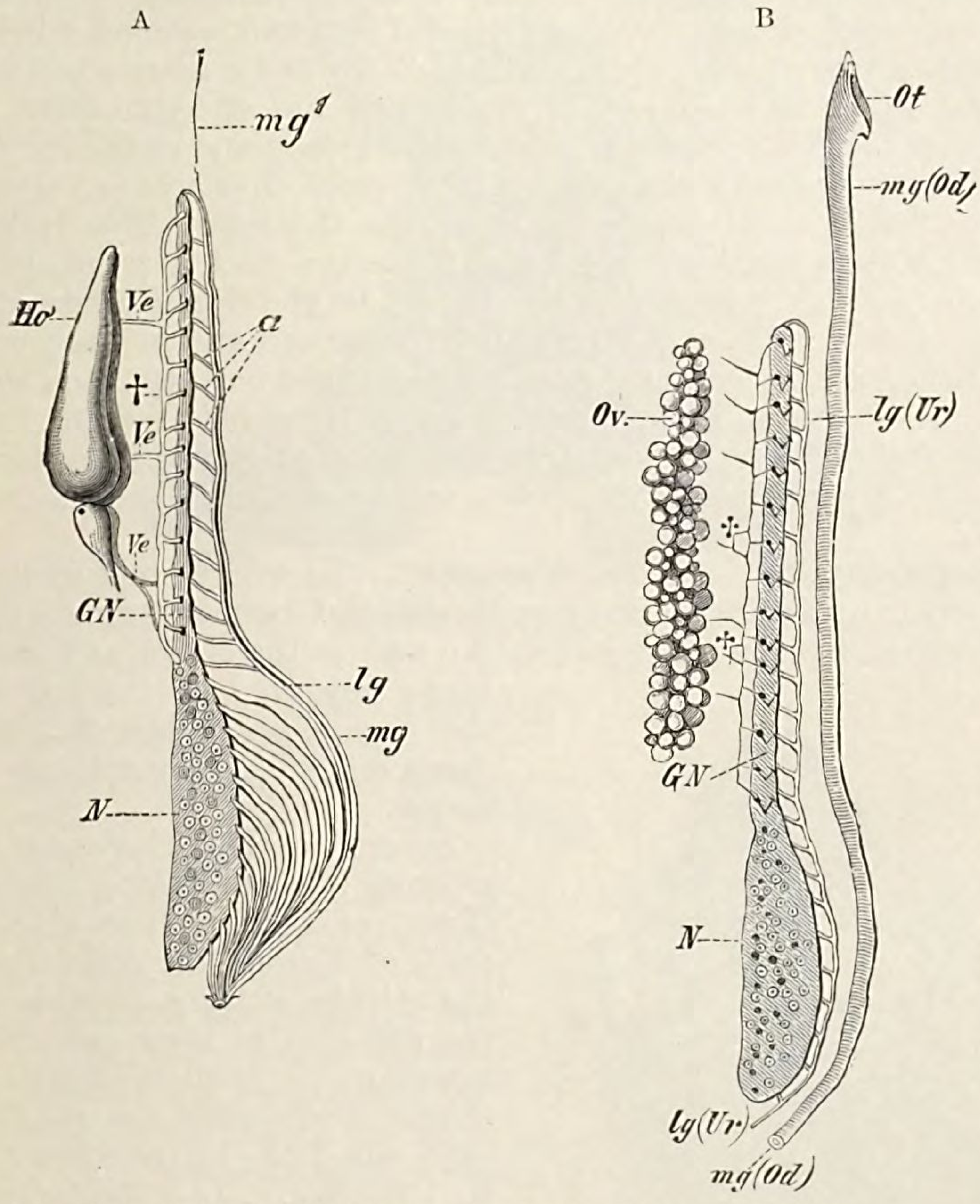


FIG. 900.—Diagrams of urinogenital organs of male (A) and female (B) **Urodele.** *a*, collecting tubes; *GN*, sexual portion of kidney; *Ho*, testis; *lg*. (*Ur*.) Wolffian duct (ureter); *mg*, *mg'*, vestigial Müllerian duct of male; *mg*. (*Od*), oviduct; *N*, non-sexual portion of kidney; *Ov*. ovary; *Ve*, vasa efferentia; †, longitudinal canal. (From Wiedersheim's *Comparative Anatomy*, after Spengel.)

non-union of the olfactory lobes. The *olfactory sacs* always open into the mouth by *posterior nares* situated behind or external to the vomers. The *eye* has no lids in the lower forms and is degenerate in the cave-dwelling Proteus and in some Gymnophiona. The Urodela, the Gymnophiona, and some Anura have no tympanic cavity or membrane, and no columella; there is, however, a *stapes*,

(Fig. 893, *St*) in the form of a nodule of cartilage inserted in the fenestra ovalis. In the perennibranchiate Urodeles and in the larvæ of the air-breathing forms *lateral sense-organs* are present. There was an extensive lateral line system, leaving its impress on the bones of the skull, in the Stegocephali.

Urinogenital Organs.—In the Urodela the *kidneys* (Fig. 900, *N*) are much elongated and are divided into two portions, a broad posterior part, the functional kidney (*GN*), and a narrow anterior sexual part connected in the male with the efferent ducts of the testis. Numerous ducts leave the kidney and open into the Wolffian (mesonephric) duct [*lg.* (*Ur.*)], which thus acts as a ureter in the female, as a urinogenital duct in the male. The oviduct [*mg.* (*Od.*)] is developed from the Müllerian duct, a rudiment of which (*mg.*, *mg'.*) occurs in the male. In the Gymnophiona the kidneys extend the whole length of the cœlome, and in the young condition are formed of segmentally arranged portions, each with a nephrostome and a glomerulus, as in Myxinoids (see p. 132). A pronephros is present in the larva, but disappears in the adult. In some Gymnophiona the cloaca can be protruded and acts as a penis.

Reproduction and **Development.**—External impregnation takes place in Anura, but in many Urodela the sperms are aggregated into *spermatophores* by glands in the wall of the cloaca, and these, being deposited on the body of the female, are taken into the cloaca and effect internal impregnation.

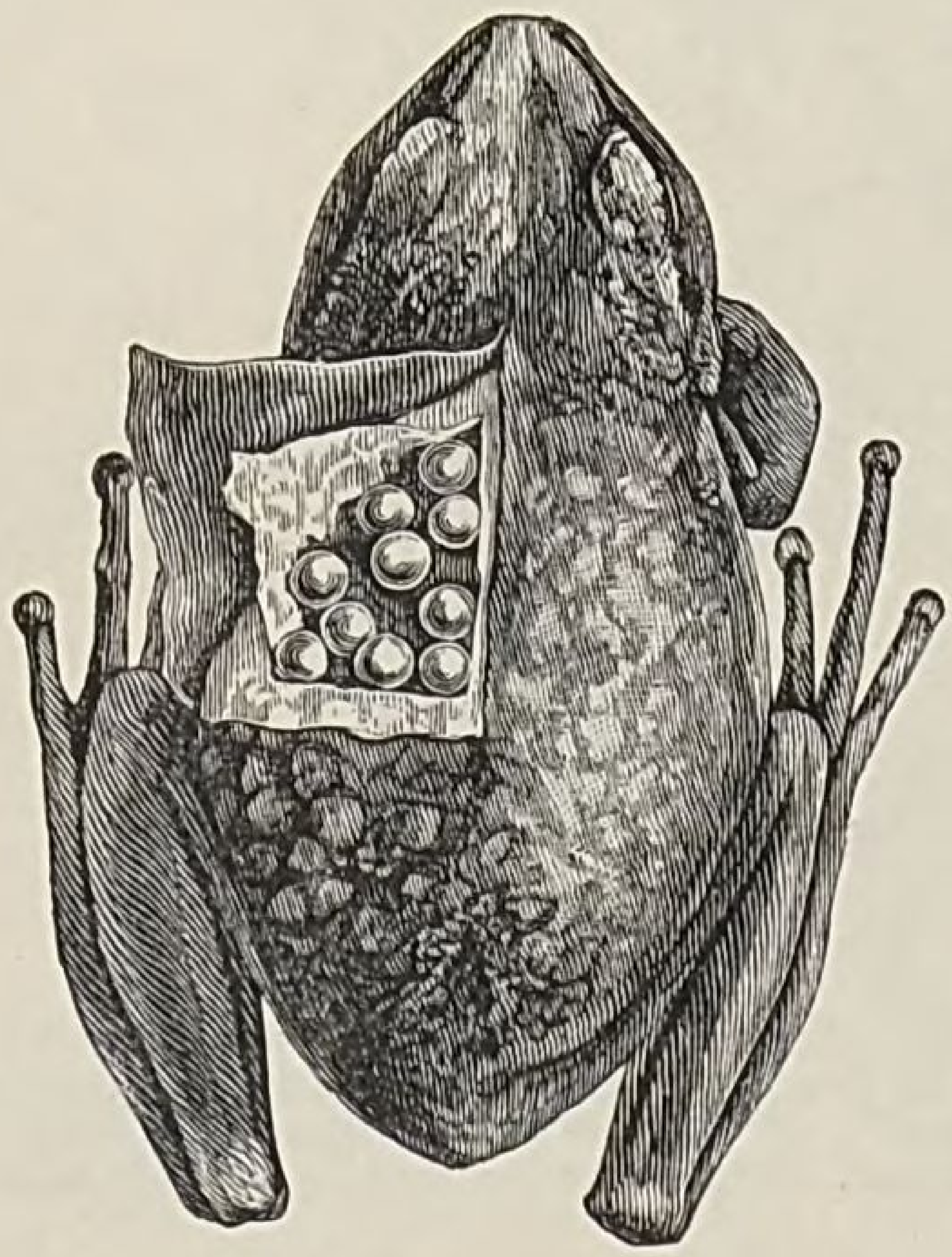


FIG. 901.—**Nototrema marsupium.** Female, with pouch opened. (From Mivart.)

Several curious instances of parental care are known. In the Obstetric Toad (*Alytes obstetricans*) of Europe the male winds the strings of eggs—formed by the adhesion of their gelatinous investment—round his body and thighs, where they are retained until the Tadpoles are ready to be hatched. In *Rhinoderma darwinii*, a little South American Frog, they are transferred by the male to his immense vocal sacs and there hatched. In another Anuran, *Nototrema* (Fig. 901), there is a pouch on the back of the female in which the eggs are stored, the young being hatched in the adult or Frog-form. Lastly, in the Surinam Toad (*Pipa americana*, Fig. 902) the skin on the back of the female becomes soft and spongy during the breeding season : the eggs are placed

on it by the male, and each sinks into a little pouch of skin covered by a gelatinous film. The embryos, which have a large yolk-sac, develop in these pouches; they never possess external gills, and are hatched in the adult form. Another Anuran, *Pseudis*

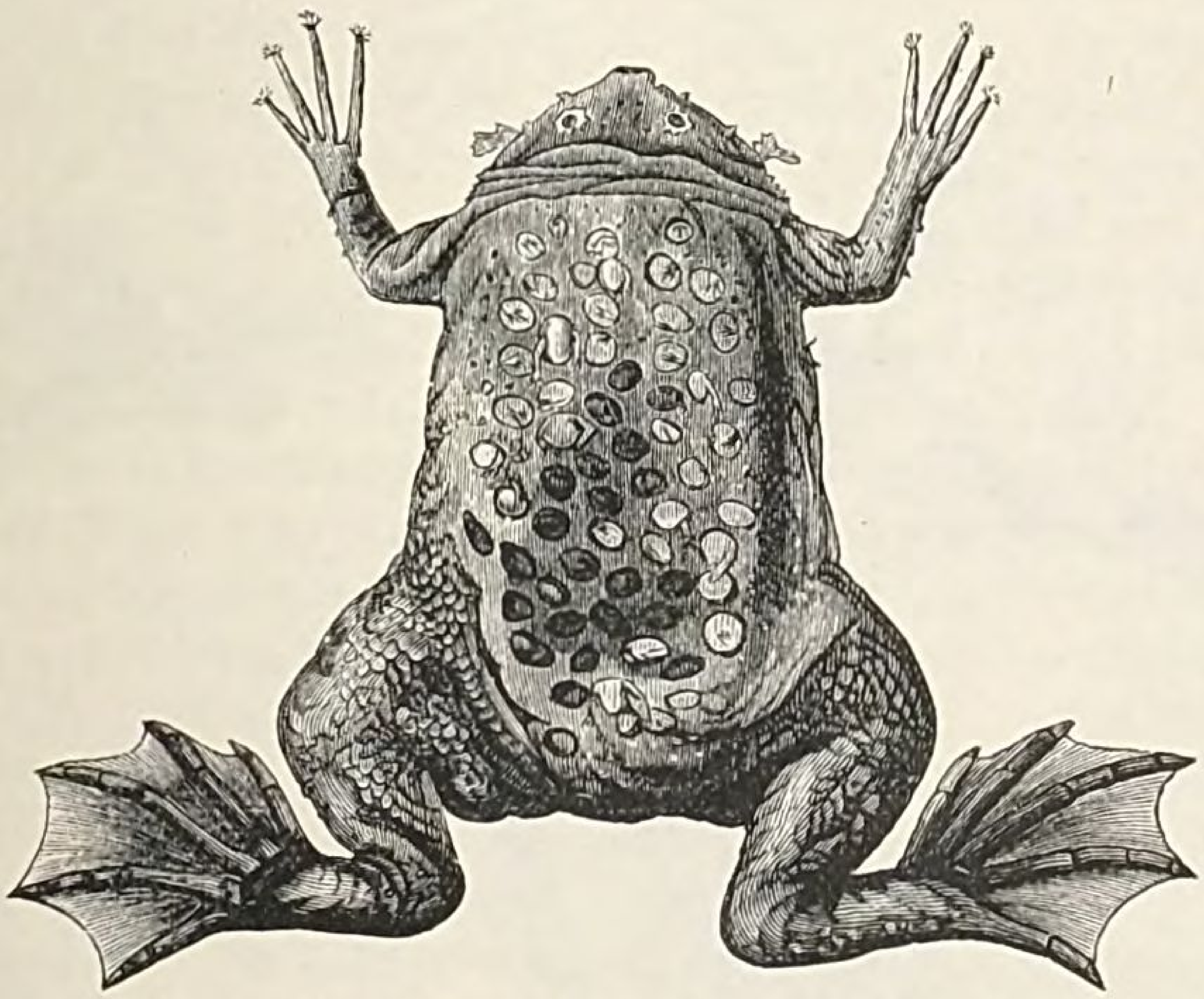


FIG. 902.—**Pipa americana.** Female. (From Mivart.)

paradoxa, is remarkable for the fact that the Tadpole is many times larger than the adult.

Some Salamanders (*S. maculosa* and *S. atra*) and a species of Cœcilia are viviparous. The young of the Black Salamander (*S. atra*) possesses long plume-like external gills during its existence in the oviduct, shedding them before birth. If, however, the unborn young is removed from the oviduct and placed in water, it swims about like an ordinary aquatic larva, losing its long gills and developing a new and shorter set. Most Gymnophiona lay their eggs in burrows, but the larvæ in some cases lead an aquatic life for a time, and during this period possess, like Tadpoles, a tail with a tail-fin which afterwards undergoes absorption. The larvæ of most Gymnophiona have long external gills (Fig. 903).

A very interesting case of *pædogenesis* is furnished by the Axolotl (*Amblystoma tigrinum*). This animal frequently undergoes no metamorphosis, but breeds in the gilled or larval state (Fig. 904). But under certain circumstances the gills are lost, the gill-slits close, and a terrestrial salamandrine form is assumed. It is to the branchiate stage that the name Axolotl properly applies; before the metamorphosis was discovered its connection with Amblystoma was not suspected, and it was placed in a distinct genus, *Siredon*, among the Perennibranchiata.

Segmentation is unequal and usually incomplete. But in Pipa, Alytes, and a Cœcilian belonging to the genus *Epicrium* there is

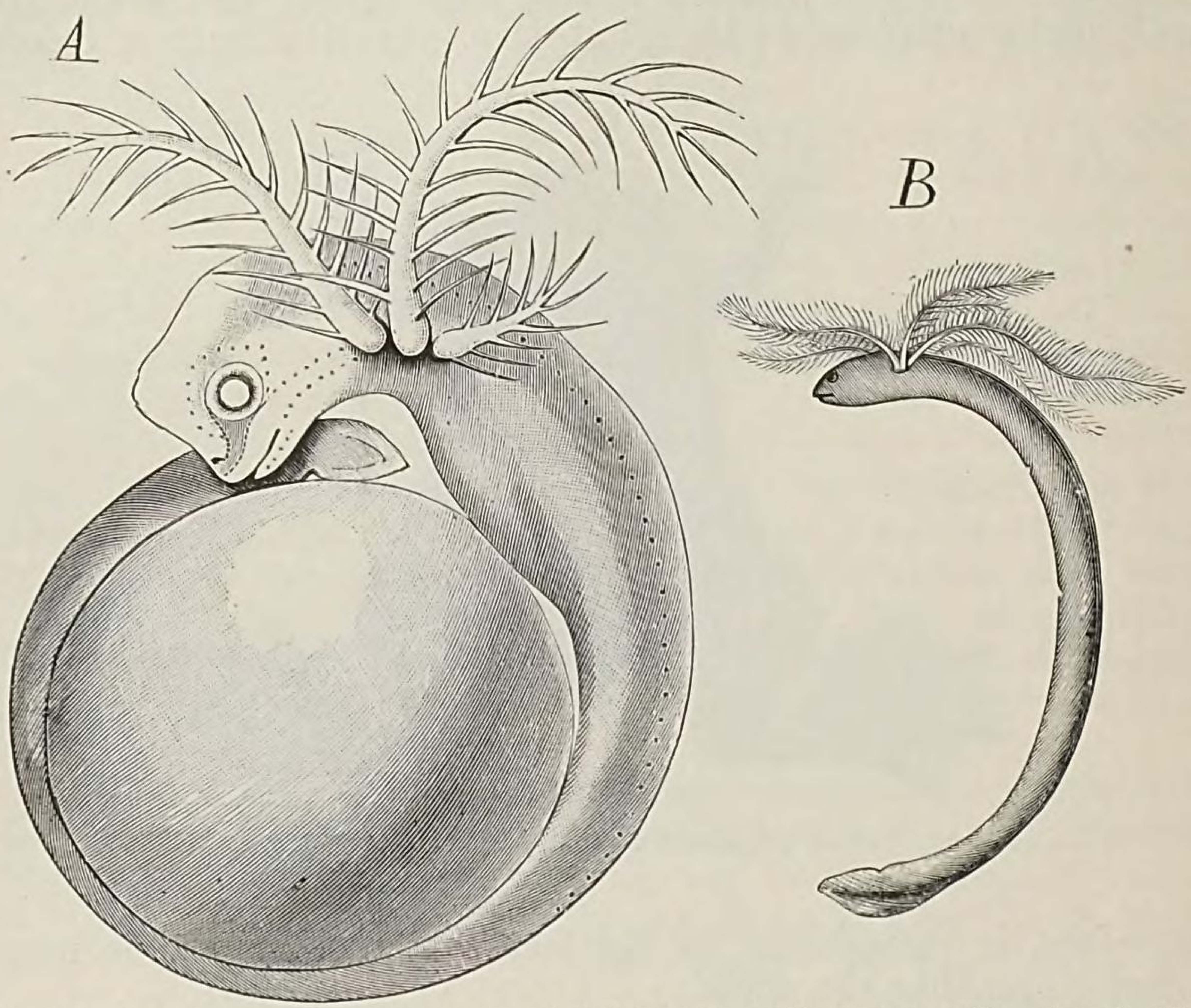


FIG. 903.—A, early. B, advanced. Larva of **Epicrium glutinosum,** with external gills. (From Wiedersheim, after Sarasin.)

a large quantity of food-yolk over which the developing embryo lies coiled very much as in the Trout (Fig. 903, A).

Distribution.—The Urodela are almost exclusively Palæarctic and Nearctic forms, occurring in North America, Europe, Asia, and

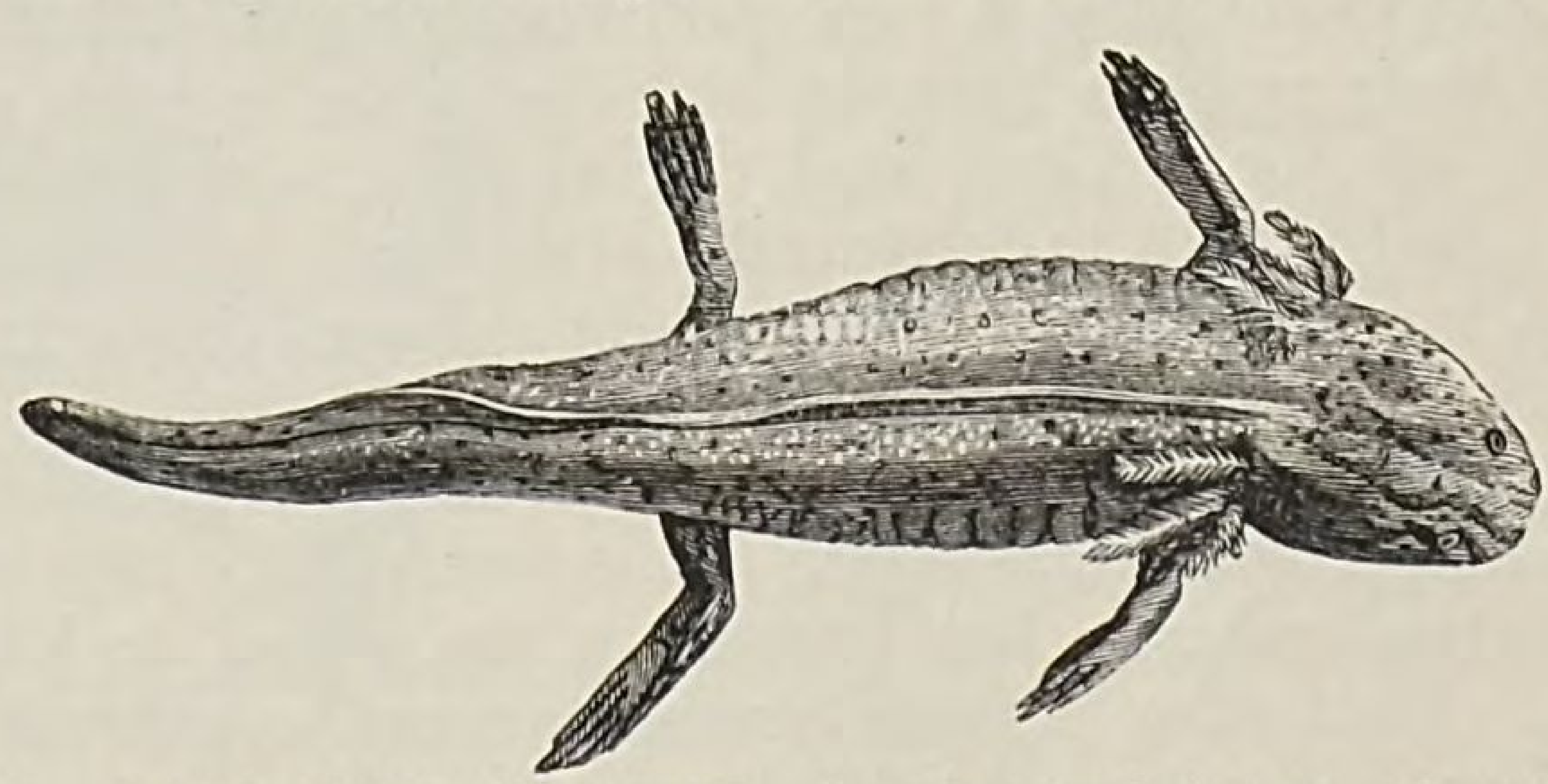


FIG. 904.—**Amblystoma tigrinum.** Larval or Axolotl stage. (From Mivart.)

North Africa: a few species extend southwards into the Neotropical and Oriental regions. The Gymnophiona, on the other hand, are mainly southern, occurring in the Neotropical, Ethiopian, and

Oriental regions, but absent in Australasia and the Pacific Islands. The Anura are almost universally distributed, and are abundant in all the greater zoo-geographical regions: they are, however, represented in New Zealand only by a single species (*Liopelma hochstetteri*) very locally distributed, and are absent in most Oceanic islands, a fact due to the fatal effects of salt water upon the eggs and embryos of Amphibia as well as upon the adult.

Remains of Stegocephali are found in considerable abundance from the Carboniferous to the Trias, and one genus extends into the Lower Jurassic, after which period the order apparently became extinct. The Urodela and Anura are not known until the Eocene, and no fossil remains of Gymnophiona have been found.

Mutual Relationships.—The perennibranchiate Urodela are undoubtedly the lowest of existing Amphibia; they lead up, through such forms as Amphiuma, with persistent gill-slits but deciduous gills, to the Land Salamanders, in which a purely terrestrial form is assumed. The Stegocephali exhibit a parallel series of modifications, some of them being perennibranchiate, others caducibranchiate. Their skull is more complex than that of the Urodela, but their vertebral column never reaches the same degree of specialisation as that of the Land Salamanders, and in some cases shows a lower grade of organisation than in any existing Amphibia. Both in their skeleton and in the distribution of their lateral sense-organs they show some affinity with the Crossopterygii. The Anura are a very specialised group: their development indicates their derivation from branchiate tailed forms, but there is no palæontological evidence on this point.

CLASS IV.—REPTILIA

Reptiles, Birds, and Mammals are associated together as having in common certain features in which they differ from lower Vertebrates. The most important of these is the occurrence in all three classes of certain embryonic membranes termed the *amnion* and the *allantois*, to be described subsequently. The term *Amniota* is, accordingly, frequently used for the group formed by these three highest classes of the Vertebrata.

The classes Reptilia and Aves are much more closely allied with one another than either of them is with the Mammalia; and the two first are sometimes associated together under the title of *Sauropsida*. The following are some of the most salient features of the Sauropsida when compared with the other Vertebrates:—

The epidermis always gives rise to important and characteristic exoskeletal structures in the form of scales or feathers; the dermis may or may not take part in the formation of an exoskeleton. The skull is well ossified: it never in the adult state contains a distinct parasphenoid. There is a single occipital condyle borne

on the basi-occipital. The basi-sphenoid is a well developed bone. The mandible articulates with the skull through the intermediation of a quadrate, and consists of five or six bones on each side. The ankle-joint is an articulation between the proximal and distal divisions of the tarsus. As in the Amphibia there is a cloaca into which the rectum and the renal and reproductive ducts open. The heart consists of two auricles and a ventricle which is sometimes incompletely, sometimes completely, divided into two parts. Branchiæ are never present at any stage. The mesonephri are never the functional renal organs of the adult, but are always replaced by metanephri. Both an amnion and an allantois are present in the embryo, the latter becoming highly vascular and acting as a temporary fœtal organ of respiration.

The class Reptilia comprises four orders having living representatives, in addition to a number of extinct groups. In the Mesozoic period the class reached its maximum both in the number of its representatives and the size which many of them attained; at that period they were very unmistakably the dominant class of the Animal Kingdom. In the Tertiary period they underwent a decline, while the Birds, and, in a yet higher degree, the Mammals, were gaining a preponderance over them. The living Reptiles are the Lizards and Chamæleons, the Tuataras, the Snakes, Tortoises and Turtles, and the Crocodiles and Alligators. Though horny epidermal scales are not by any means present in all the Reptiles, their occurrence as a complete covering is characteristic of the group and peculiar to it. When scales are not present, the epidermis is always hardened and cornified so as to form plates of horny material, such as the horny plates of the Tortoises, which protect the underlying soft parts from injury and desiccation. Bony plates are frequently present as well. In most respects the internal structure of the Reptilia shows a very decided advance on that of the Amphibia. The skull is more completely ossified, as well as the pectoral and pelvic arches, and both vascular and nervous systems show a higher grade of organisation.

1. Example of the Class.—A Lizard (*Lacerta*).

The most striking external differences between the Lizard (Fig. 905) and the Frog are the covering of scales, the comparative smallness of the head, and the presence of a distinct neck, the great length of the caudal region, the shortness of the limbs, and the approximate equality in length of the anterior and posterior pairs. The anterior limbs are situated just behind the neck, springing from the trunk towards the ventral surface. The fore-limb, like that of the Frog, is divided into three parts, the upper-arm or *brachium*, the fore-arm or *anti-brachium*, and the hand or *manus*; there are five digits provided with horny claws, the first digit or

pollex being the smallest. The hind-limbs arise from the posterior end of the trunk towards the ventral aspect; each, like that of the Frog, consists of three divisions—thigh or *femur*, shank or *crus*, and foot or *pes*. The pes, like the manus, terminates in five clawed digits, of which the first or hallux is the smallest. The head is somewhat pyramidal, slightly depressed: the openings of the external nares are situated above the anterior extremity. The mouth is a wide slit-like aperture running round the anterior border of the head. At the sides are the eyes, each provided with upper and lower opaque movable eyelids and with a transparent third eyelid or *nictitating membrane*, which, when withdrawn, lies

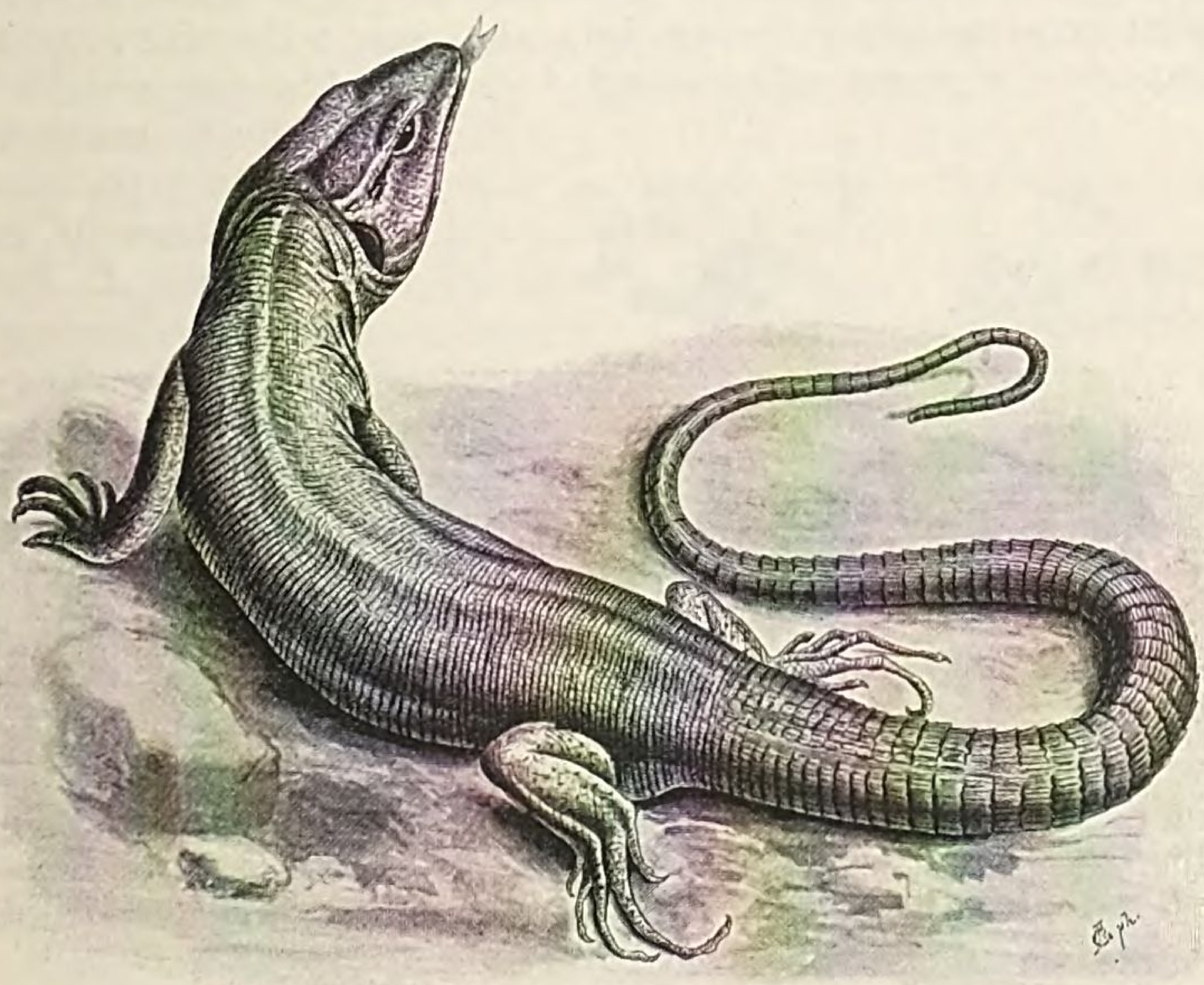


FIG. 905.—**Lacerta viridis.** (After Brehm.)

in the anterior angle of the orbit. Behind the eye is a circular brown patch of skin—the *tympanic membrane*—corresponding closely to that of the Frog, but somewhat sunk below the general level of the skin. The trunk is elongated, strongly convex dorsally, flatter at the sides and ventrally. At the root of the tail on the ventral surface is a slit-like transverse aperture—the *anus* or *cloacal aperture*. The tail is cylindrical, thick in front, gradually tapering to a narrow posterior extremity; it is nearly twice as long as the head and trunk together.

There is an **exoskeleton** of horny epidermal *scales* covering all parts. In size these differ in different positions. On the dorsal

surface of the trunk they are small, hexagonal, and indistinctly keeled. On the ventral surface they are larger and are arranged in eight longitudinal rows. Immediately in front of the cloacal aperture is a large *pre-anal plate*. A collar-like ridge of larger scales surrounds the throat. On the tail the scales are elongated, keeled, and arranged in regular transverse (annular) rows, giving the tail a ringed appearance. On the surface of the limbs the scales of the pre-axial side are larger than those of the post-axial. The scales on the upper surface of the head (*head shields*) are large, and have a regular and characteristic arrangement.

Endoskeleton.—The *vertebral column* is of great length and made up of a large number of vertebræ. It is distinctly marked out into regions, a cervical of eight vertebræ, a thoracico-lumbar of twenty-two, a sacral of two, and a caudal of a considerable, but indefinite, number. A vertebra from the anterior thoracic region (Fig. 906, *A*, *B*) presents the following leading features. The centrum (*cent.*) is elongated and strongly *procœlous*, *i.e.* the anterior surface is concave, the posterior convex; the neural arch bears a short neural spine (*sp*). There are pre- and post-zygapophyses (*pr.zy*, *pt.zy*), the former with their articular surfaces directed upwards, the latter downwards. On each side at the junction of centrum and neural arch is a facet—the *capitular facet*—for the articulation of a rib. The cervical vertebræ in general are similar in essential respects to those of the trunk, but are somewhat shorter. The first two, however, differ greatly from the others. The first is the *atlas* (*C*, *D*). It has no distinct centrum, but is in the form of a ring; ventrally on its anterior face it bears a smooth articular facet for the occipital condyle of the skull. It consists of three distinct ossifications, one ventral, the others dorso-lateral: the latter do not quite meet dorsally, being separated by a space bridged over by membrane. The second or *axis* (*E*) has a short conical process—the *odontoid process* (*od*)—projecting forwards from its centrum. In the natural position of the parts the odontoid process, which is a part of the centrum of the atlas, and is not actually fused with, though firmly fixed to, the axis, lies in the lower or ventral part of the opening of the atlas, separated

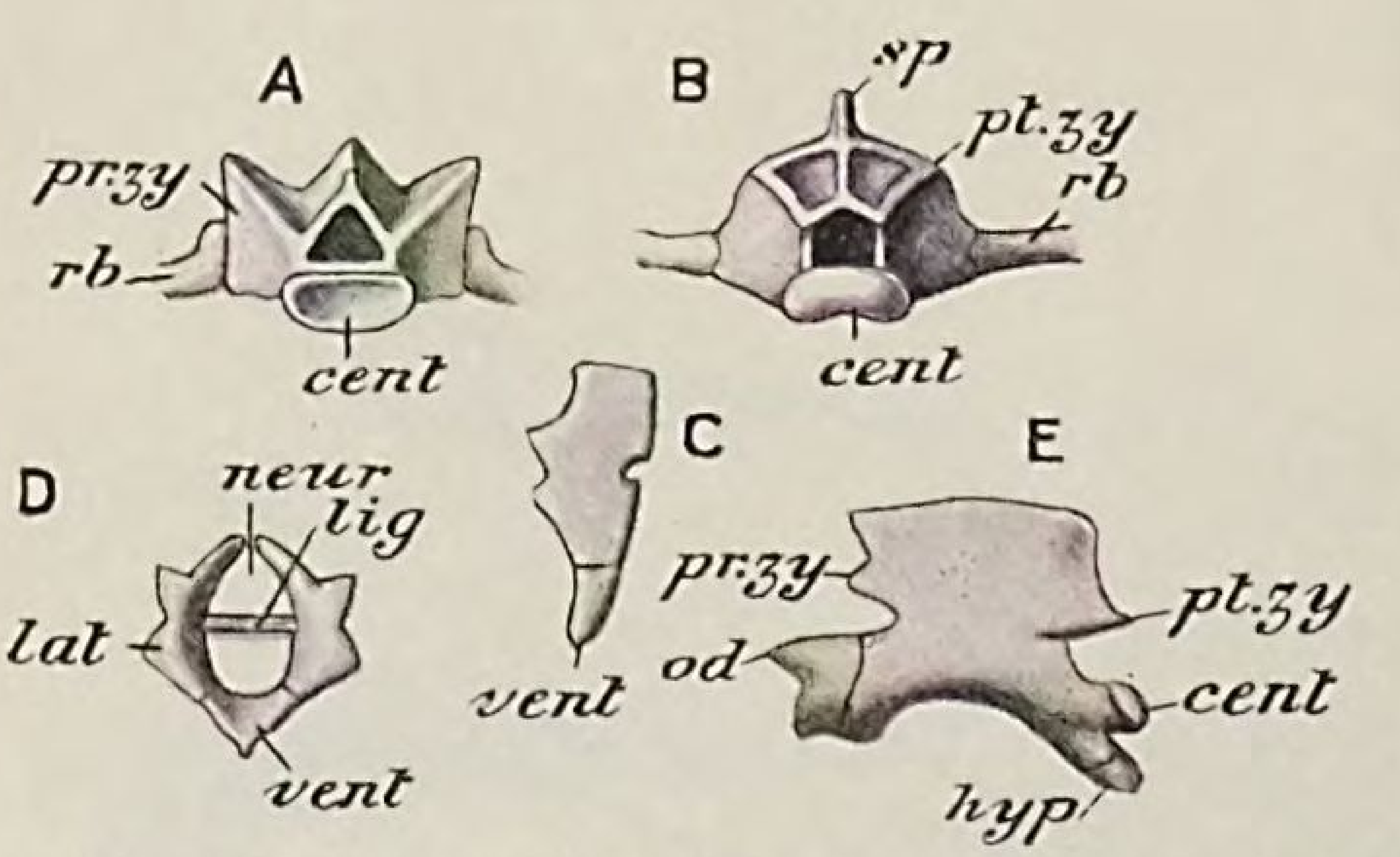


FIG. 906.—Vertebræ of **Lizard**. *A*, anterior, *B*, posterior, view of a thoracic vertebra; *C*, lateral, *D*, anterior, view of atlas vertebra; *E*, lateral view of axis. *cent.* centrum; *hyp.* hypapophysis of axis; *lat.* lateral piece of atlas; *lig.* ligamentous band dividing the ring of the atlas into two; *neur.* neural arch of atlas; *od.* odontoid process; *pr. zy.* pre-zygapophysis; *pt. zy.* post-zygapophysis; *rb.* rib; *sp.* spine; *vent.* ventral piece of atlas.

by a ligamentous band from the upper portion, which corresponds to the neural arch, and lodges the anterior end of the spinal cord. On the ventral surface of the axis, and of each of the following five or six vertebræ, is a distinct bony nodule, sometimes termed the *hypapophysis* (*hyp*). The sacral vertebræ have short centra and strong expanded processes—the *transverse processes*—which abut against the ilia; these are separately ossified, and are to be looked upon as *sacral ribs*. The anterior caudal vertebræ are like the sacral, but have the centra longer, the transverse processes more slender, and the neural spines longer. The posterior caudal vertebræ become gradually smaller as we pass backwards, and the various processes reduced in prominence, until, when we get to the end of the tail, the whole vertebra is represented merely by a rod-like centrum. Attached to the ventral faces of the centra of a number of the anterior caudal vertebræ are Y-shaped bones—the *chevron bones*—the upper limb of the Y articulating with the vertebra, while the lower limb extends downwards and backwards. In nearly all the caudal vertebræ the centrum is crossed by a narrow transverse unossified zone through which the vertebra readily breaks. The ribs are slender curved rods, the vertebral end of each of which articulates with one of the capitular facets of the corresponding vertebra. The ribs of the five anterior thoracic vertebræ are connected by means of cartilaginous *sternal ribs* with the sternum. The posterior thoracic ribs do not reach the sternum, the sternal ribs being very short and free at their ventral ends. The *cervical ribs*, which are present on all the cervical vertebræ with the exception of the first three, are all shorter than the thoracic ribs, and none of them are connected with the sternum. Thus, as regards the structure of the vertebræ themselves, there is nothing to distinguish the posterior cervical from the anterior thoracic; but, for convenience of description, the first thoracic is defined as the first vertebra having ribs connected with the sternum.

The *sternum* (Fig. 908, *st*) is a rhomboidal plate of cartilage with a small central space, or *fontanelle*, completed by membrane. Posteriorly it is produced into two slender flattened processes. On its antero-lateral borders are articular surfaces for the bones of the pectoral arch, and on its postero-lateral borders and the processes are small facets for the sternal ribs.

In the *skull* (Fig. 907) the chondrocranium, though persistent, is replaced by cartilage bones to a much greater extent than in the Frog, and the number of membrane bones is much greater. On the dorsal and lateral surface are a large number of dermal roofing bones. At the posterior end the rounded aperture of the foramen magnum (*for. mag*) is surrounded by four bones—*basi-occipital* (*bas. oc*) below, *ex-occipitals* (*ex. oc*) at the sides and *supra-occipital* (*supr. oc*) above. The basi-occipital forms the

floor of the most posterior portion of the cranial cavity; posteriorly it bears a rounded prominence, the *occipital condyle* (*oc. cond*).

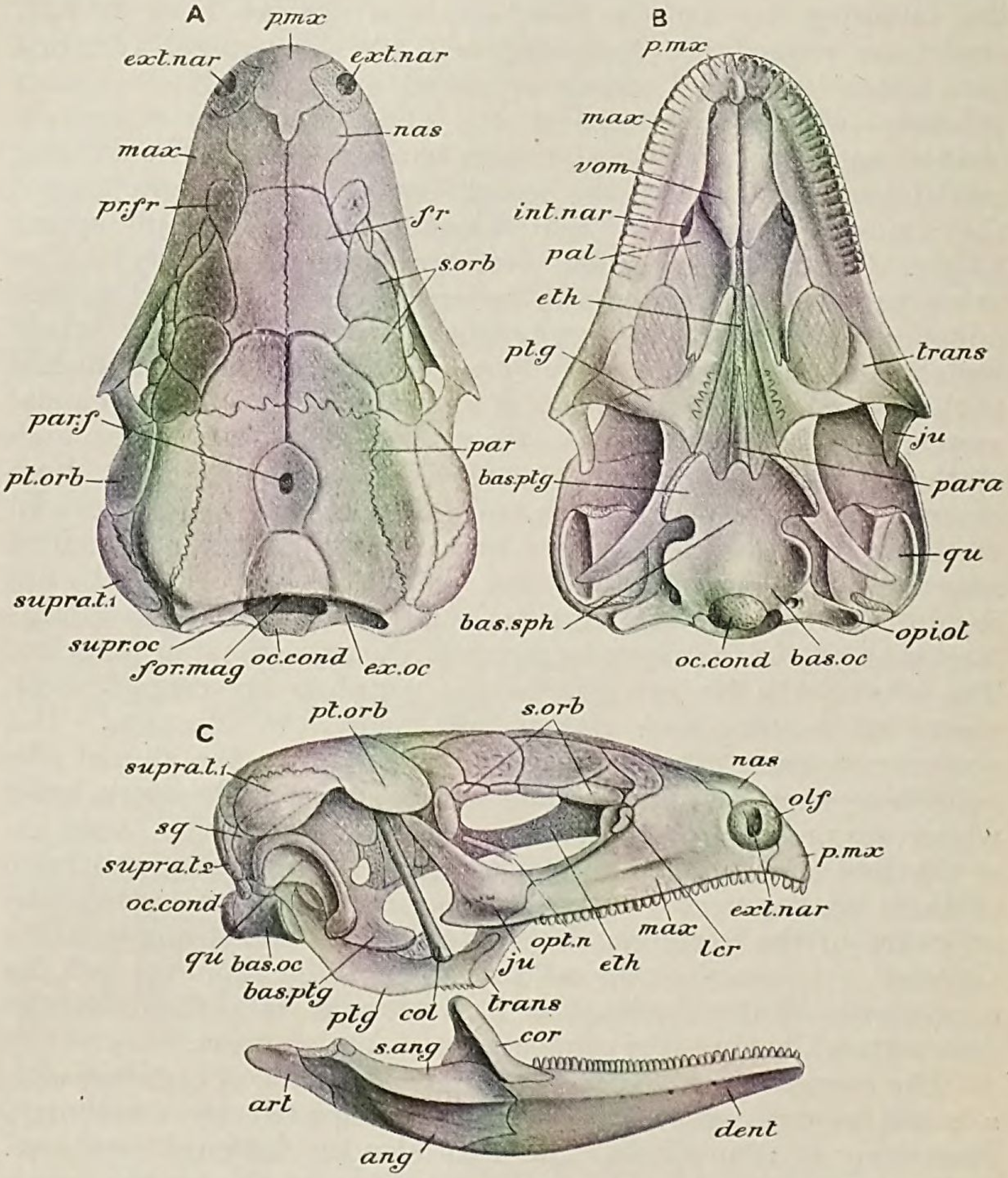


FIG. 907.—Skull of **Lacerta agilis.** A, from above; B, from below; C, from the side. *ang.* angular; *art.* articular; *bas. oc.* basi-occipital; *bas. ptg.* basi-pterygoid processes; *bas. sph.* basi-sphenoid; *col.* epi-pterygoid; *cor.* coronary; *dent.* dentary; *eth.* ethmoid; *ex. oc.* ex-occipital; *ext. nar.* external nares; *for. mag.* foramen magnum; *fr.* frontal; *int. nar.* internal nares; *ju.* jugal; *lcr.* lacrymal; *max.* maxilla; *nas.* nasal; *oc. cond.* occipital condyle; *olf.* olfactory capsule; *op. ot.* opisthotic; *opt. n.* optic nerve; *pal.* palatine; *par.* parietal; *para.* parasphenoid; *par. f.* parietal foramen; *p. mx.* pre-maxillæ; *pr. fr.* pre-frontal; *ptg.* pterygoid; *pt. orb.* post orbital; *qu.* quadrate; *s. ang.* supra-angular; *s. orb.* supra-orbitals; *sq.* squamosal; *supra* t^1. supra-temporal 1; *supra* t^2. supra-temporal 2; *trans.* transverse; *supra. oc.* supra-occipital; *vom.* vomer. (After W. K. Parker.)

In front of it, forming the middle portion of the floor of the cranial cavity, is the basi-sphenoid (*bas. sph*), not represented in the Frog, in front of which again is a membrane bone, the *parasphenoid*

(*para*), corresponding to the bone of the same name in the Frog, and Trout, but here much reduced in size and importance, and ankylosed with the basi-sphenoid.

In the wall of the auditory capsule are three ossifications—*pro-otic*, *epi-otic* and *opisthotic* (*op. ot*). The first remains distinct, the second becomes merged in the supra-occipital, and the third in the ex-occipital. The ex-occipital and opisthotic are produced outwards as a pair of prominent horizontal processes, the *parotic processes.*

The large orbits are closely approximated, being separated only by a thin vertical *inter-orbital septum.* The cranial cavity is roofed over by the *parietals* (*par*) and *frontals* (*fr*). The former are united together; in the middle is a small rounded aperture—the *parietal foramen* (*par. f*). The frontals remain separated from one another by a median *frontal suture:* between them and the united parietals is a transverse *coronal suture.* The nasal cavities are roofed over by a pair of *nasals* (*nas*). A small *pre-frontal* (*pr. fr.*) lies in front of the frontal, and helps to bound the orbit anteriorly, and another small bone—the *lacrymal* (*lcr*)—perforated by an aperture for the lacrymal duct, lies at the anterior extremity of the orbit, just within its border. A row of small bones—the *supra-orbitals* (*s. orb*)—bounds the orbit above, and behind is a *post-orbital* (*pt. orb*) articulating with the frontal. Just behind the latter are two *supra-temporal* bones (*supra t*[1], *supra t*[2]), in close relation to which is the *squamosal* (*sq*). At the anterior extremity of the snout is a median bone formed by the coalescence of the two *pre-maxillæ* (*p. mx*); this bears the four anterior teeth of each side. On each side behind the premaxilla is the *maxilla* (*max*), consisting of two portions, an *alveolar* bearing all the rest of the teeth, and a *palatine* extending inwards on the roof of the mouth, together with an ascending process articulating with the nasal and pre-frontal above. Articulating behind with each maxilla is a *jugal* (*ju*) which forms the posterior half of the ventral boundary of the orbit. The *quadrate* (*qu*) articulates movably with the parotic process, and bears at its distal end the articular surface for the mandible.

In the anterior portion of the roof of the mouth, articulating in front with the pre-maxillæ and maxillæ, are the vomers (*vom*). Behind them and embracing them posteriorly are the flat *palatines* (*pal*). The elongated *pterygoids* (*pt.g*) articulate in front with the posterior extremities of the palatines: behind each articulates with the corresponding *basi-pterygoid process* (*bas. ptg*) of the basi-sphenoid; and sends back a process which becomes applied to the inner face of the quadrate. A stout bone which extends between the maxilla externally and the pterygoid internally is termed the *transverse* (*trans*). Extending nearly vertically downwards from the pro-otic to the pterygoid is a slender rod of bone, the *epi-pterygoid* (*col*).

The *columella* is a small rod partly composed of cartilage and partly of bone, the outer end of which is fixed into the inner surface of the tympanic membrane, while the inner is attached to a small aperture, the *fenestra ovalis*, in the outer wall of the auditory capsule between the pro-otic and the opisthotic.

Certain depressions or fossæ and apertures or foramina are to be observed in the skull. The foramen magnum, the parietal foramen, and the orbits have been already mentioned. The *posterior temporal fossa* is situated on either side of and above the foramen magnum, bounded above and externally by the roofing bones, and on the inner side by the bones of the occipital region. The *inferior temporal fossa* is bounded internally by the pterygoid, and is separated from the palatine foramen by the transverse. The *lateral temporal fossa* is the wide space in the side wall of the skull behind the orbit; the bony bar which limits it above is the *superior temporal arch*; a bony *inferior temporal arch* is here absent. The *tympano-eustachian fossa*, situated in the auditory region, is bounded by the bones of that region together with the quadrate. The *posterior* or *internal nares* are bounded posteriorly by the palatines. The *anterior* or *external nasal aperture* is situated at the anterior extremity of the skull bounded by the nasals and pre-maxillæ.

Each ramus of the *mandible* consists of six bony elements in addition to the slender persistent *Meckel's cartilage*. The proximal element is the *articular* (*art*) which bears the articular surface for the quadrate, and is produced backwards into the *angular process*. The *angular* (*ang*) is a splint-like bone covering the ventral edge and the lower half of the outer surface of the articular. The *supra-angular* (*s. ang*) overlies the dorsal edge and upper half of the outer surface of the articular. The *dentary* (*dent*) forms the main part of the distal portion of the mandible, and bears all the mandibular teeth. The *splenial* is a flat splint applied to the inner face of the dentary. The *coronary* (*cor*), a small, somewhat conical bone, forms the upwardly directed *coronoid process* immediately behind the last tooth. All these, with the exception of the articular, are membrane bones.

The *hyoid arch* (*vide* Fig. 913; *b. hy*) consists (1) of a median cartilaginous rod, the *basi-hyal*, (2) of the *anterior cornua*, elongated cartilaginous rods which, connected ventrally with the basi-hyal, curve round the gullet and end in close relation with the ventral surface of the auditory capsule, (3) of the *middle cornua*, rods of cartilage ossified at their proximal ends, and (4) of the *posterior cornua*, cartilaginous rods arising from the posterior edge of the basi-hyal and passing backwards and outwards. The middle cornua are vestiges of the first, the posterior of the second, branchial arch.

In the *pectoral arch* (Fig. 908) the *coracoids* are flat bones articulating with the antero-lateral border of the sternum, and

bearing the ventral half of the glenoid cavity (*glen*) for the head of the humerus; a large gap or fenestra divides each into a narrow anterior portion—the *pro-coracoid* (*pr. cor*) and a broader posterior portion, the *coracoid* proper (*cor*). The *scapulæ* (*sc*) articulate with the outer ends of the coracoids, and each bears the dorsal half of the glenoid cavity. Dorsally the scapulæ become expanded, and each has connected with it a thin plate of partly calcified cartilage—the *supra-scapula* (*supra. sc*), which extends inwards towards the spinal column on the dorsal aspect of the body. An element not hitherto met with is the *interclavicle* or *episternum* (*epist*), a cross-shaped membrane bone, the stem of which is longitudinal and closely applied to the ventral surface of the sternum, while the cross-piece is situated a little in front of the glenoid cavities. The *clavicles* (*cl*) are flat curved bones articulating with one another in the middle line and also with the anterior end of the interclavicle. The bones of the fore-limb consist of a proximal bone or *humerus*, a middle division composed of two bones—the *radius* and *ulna*, and a distal division or *manus*. In the natural position of the parts the humerus is directed, from the glenoid cavity with which it articulates, backwards upwards and outwards; the radius and ulna pass from their articulation with the humerus downwards and slightly forwards, while the manus has the digits directed forwards and outwards. When the limb is extended at right angles to the long axis of the trunk, it presents, like that of the Frog, dorsal and ventral surfaces, and pre-axial and post-axial borders. In this position the radius is seen to be pre-axial, the ulna post-axial. In the natural position the pre-axial border of the humerus is external, and the distal end of the forearm is rotated in such a way that, while the pre-axial border looks forwards and outwards at the proximal end, it looks

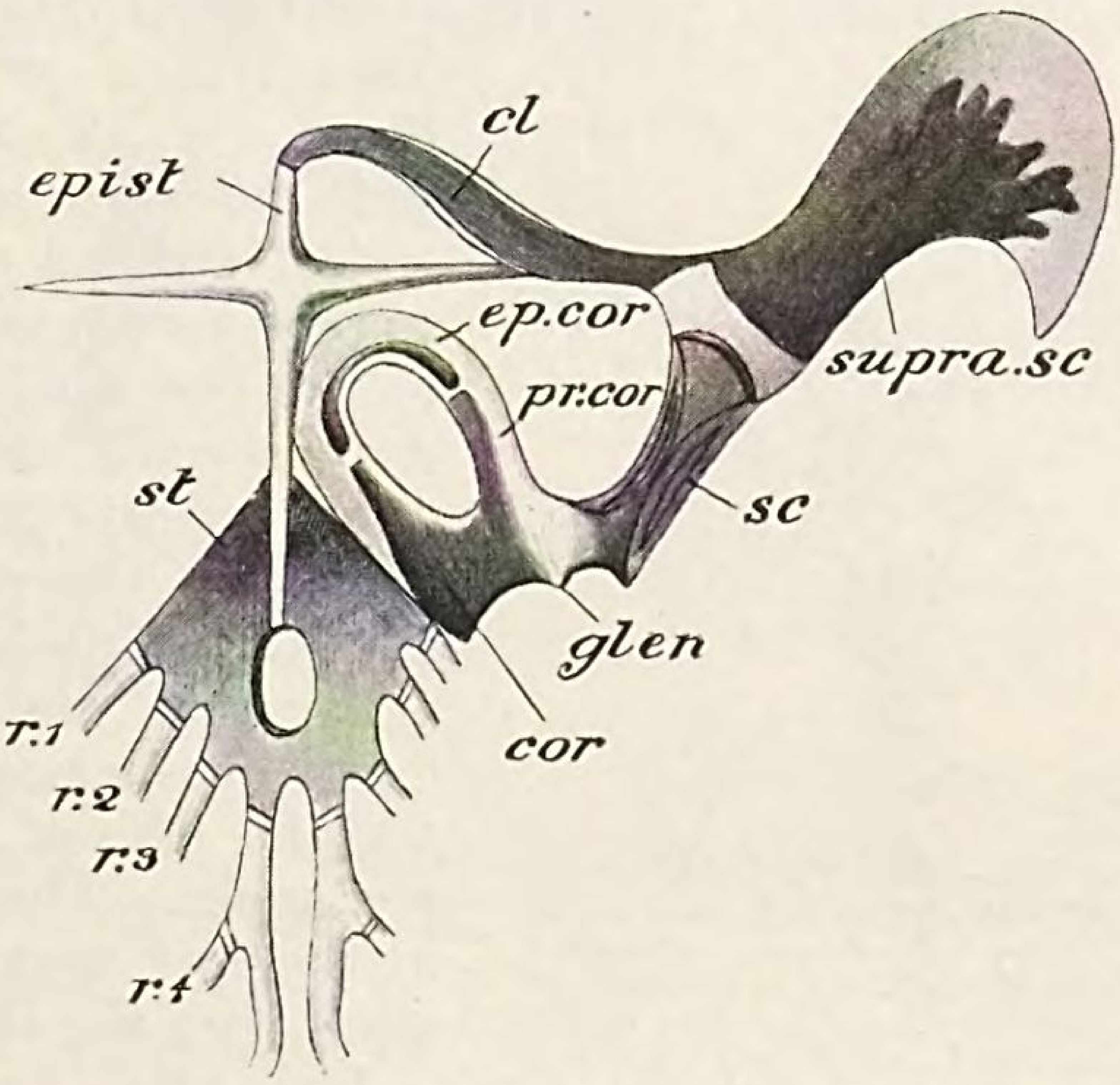


FIG. 908.—Pectoral arch and sternum of **Lacerta agilis.** *cl.* clavicle; *cor.* coracoid; *ep. cor.* epicoracoid; *epist.* episternum; *glen.* glenoid cavity for head of humerus; *pr. cor.* pro-coracoid; *r*1.—*r*4. first to fourth sternal ribs; *sc.* scapula; *st.* sternum; *supra. sc.* supra-scapula. (After Hoffmann.)

directly inwards at its distal end, the manus being rotated so that its pre-axial border looks inwards.

The *humerus* is a long bone consisting of a *shaft* and two *extremities*, each of the latter being formed of an *epiphysis* of calcified cartilage, the proximal rounded, the distal pulley-like (*trochlea*) with two articular surfaces, one for the radius and the other for the ulna. The *radius* is a slender bone consisting, like the humerus, of a shaft and two epiphyses; the distal extremity has a concave articular surface for the carpus, and is produced pre-axially into a *radial styloid process*. The proximal end of the *ulna* is produced into an upwardly directed process—the *olecranon*. The distal end bears a convex articular surface for the carpus. The *carpus* (Fig. 909) is composed of ten small polyhedral or rounded carpal bones. These consist of a proximal row containing three, viz., the *radiale* (*r*), *ulnare* (*u*), and *intermedium* (*i*), of a *centrale* (*c*), and of a distal row of five (1–5); with an accessory or *pisiform* (†) bone attached to the distal epiphysis of the ulna on its post-axial side. The first digit or *pollex* consists of a metacarpal and two phalanges, the second of a metacarpal and three phalanges, the third of a metacarpal and four phalanges, the fourth of a metacarpal and five phalanges, and the fifth of a metacarpal and three phalanges. The number of phalanges in the first four digits is, therefore, one more than the number of the digit.

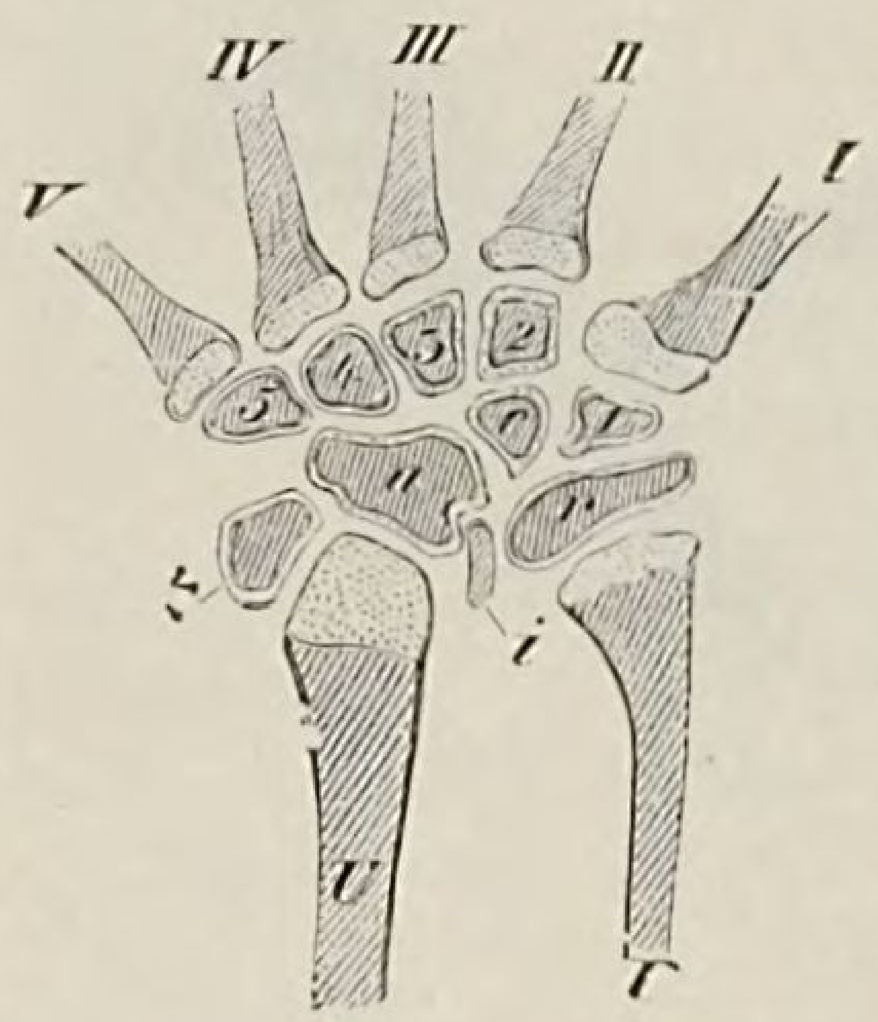


FIG. 909.—Carpus of **Lacerta agilis,** (left) from above. *R.* radius; *U.* ulna; *c.* centrale; *i.* intermedium; *r.* radiale; *u.* ulnare; 1—5, the five distal carpals; †, pisiform; *I—V*, the five metacarpals. (After Wiedersheim.)

The *pelvic arch* (Fig. 910) consists of two triradiate bones, the *ossa innominata*, each ray being a separate bone. On the outer side at the point from which the rays diverge is a concave articular surface—the *acetabulum* (*Ac*)—for the head of the humerus. From the region of the acetabulum one of the rays, the *ilium* (*I*), a compressed rod, passes upwards and backwards to articulate with the sacral region of the spinal column. A second ray—the *pubis* (*P*)—passes downwards and forwards to meet its fellow in the middle line, the articulation being termed the *pubic symphysis*. In the middle in front, between the anterior ends of the pubes, is a small nodule of calcified cartilage, the *epi-pubis* (*Cep*). The third ray or *ischium* (*Is*) runs downwards and backwards, and articulates with its fellow in the *ischiadic symphysis*, the ventral ends of the two bones being separated by a plate of calcified cartilage. Between the pubes and ischia is a wide space divided by a median ligament (*lg*) into a pair of apertures which are termed the *obturator foramina*. A small rod of bone, the *os cloacæ*, or hypo-

ischium (*Hp Is*), passes backwards from the ischiadic symphysis and supports the ventral wall of the cloaca.

The hind-limb consists, like the fore-limb, of three divisions; these are termed respectively the proximal or *femur*, the middle or *crus*, and the distal or *pes*. The proximal division consists of one bone, the *femur*; the middle division of two, the *tibia* and *fibula*; the distal of the *tarsal* and *metatarsal* bones and the *phalanges*. When the limb is extended at right angles with the trunk, the tibia is pre-axial and the fibula post-axial: in the natural position of the parts the pre-axial border is internal in all three divisions of the limb. The *femur* is a stout bone consisting of a shaft and two epiphyses. The proximal epiphysis develops a rounded *head* which fits into the acetabulum; near it on the pre-axial side is a prominence, the *lesser trochanter*, and a nearly obsolete prominence on the post-axial side represents the *greater trochanter*. The distal extremity is pulley-shaped, with internal and external prominences or *condyles* for articulation with the tibia; immediately above the external condyle is a prominence or tuberosity for articulation with the fibula. The *tibia* is a stout, curved bone, along the anterior (dorsal) edge of which runs a longitudinal ridge, the *cnemial ridge*: the proximal extremity presents two articular surfaces for the condyles of the femur. The *fibula* is a slender bone, the proximal end articulating with the external tuberosity of the femur, the distal with the tarsus.

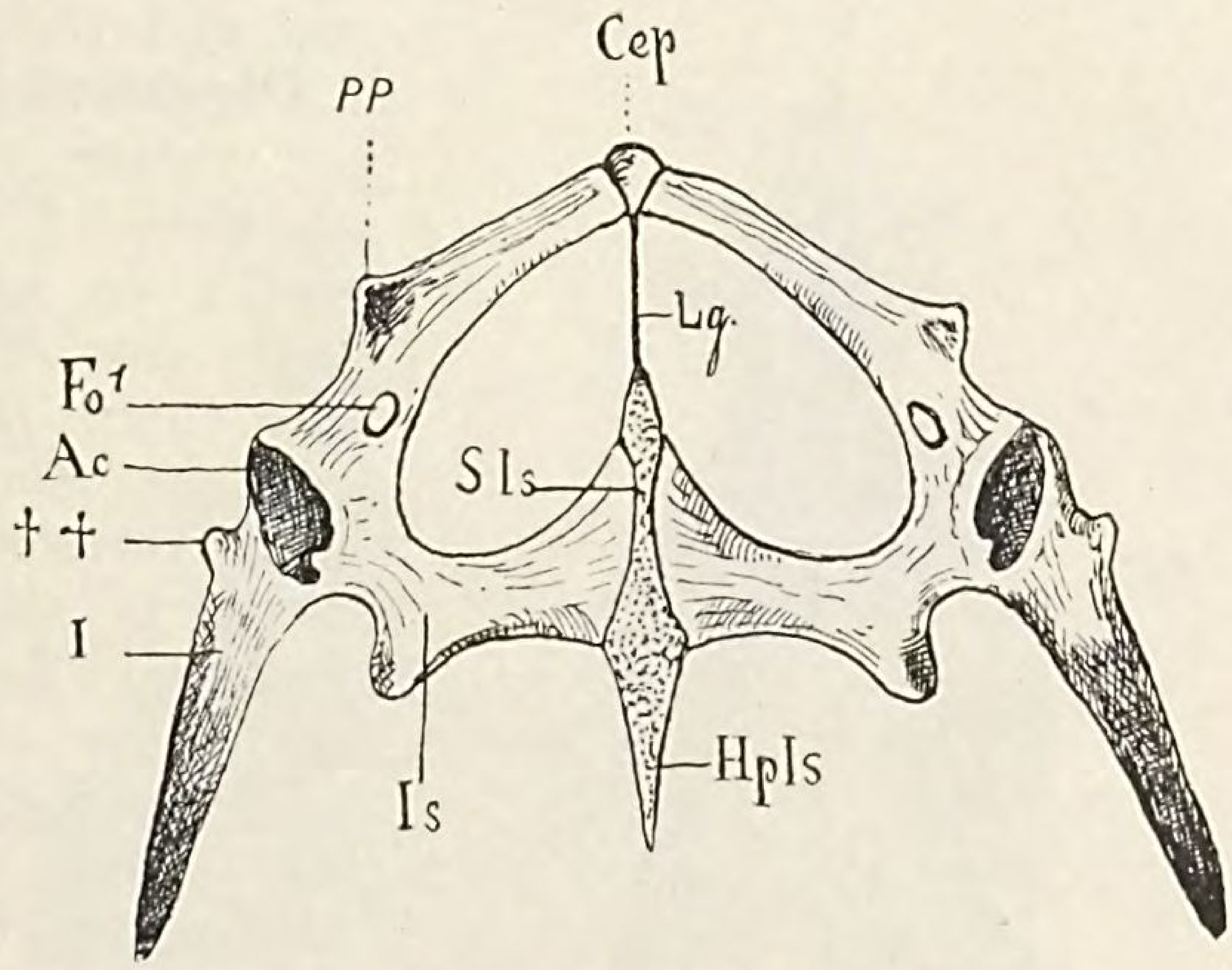


FIG. 910.—Pelvis of **Lacerta vivipara**, from the ventral side. *Ac.* acetabulum; *Cep.* epi-pubis: *Fo'.* foramen for obturator nerve; *Hp.Is.* hypo-ischium; *I.* ilium; † †, process representing the pre-acetabular part of the ilium: *Is.* ischium; *P.* pubis; *PP.* pre-pubis. (After Wiedersheim.)

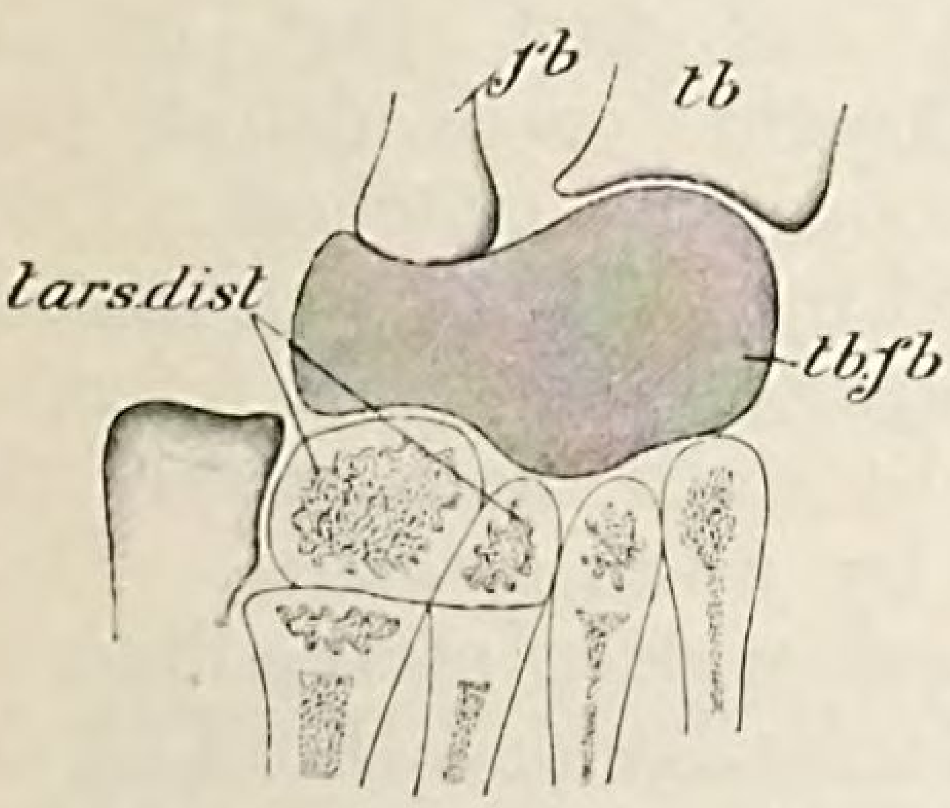


FIG. 911.—Tarsus of **Lacerta agilis.** *fb.* fibula; *tb.* tibia; *tb.fb.* tibio-fibulare; *tars. dist.* distal tarsals. (After Gegenbaur.)

The *tarsus* (Fig. 911) comprises only three bones in the adult,

one large proximal bone, the *tibio-fibulare* (*tb. fb*), and two smaller distal (*tars. dist*). Each digit consists of a metatarsal bone and phalanges, the number of the latter being two, three, four, five, and three. The first and second metatarsals articulate with the tibial side of the tibio-fibulare: the rest with the distal tarsals.

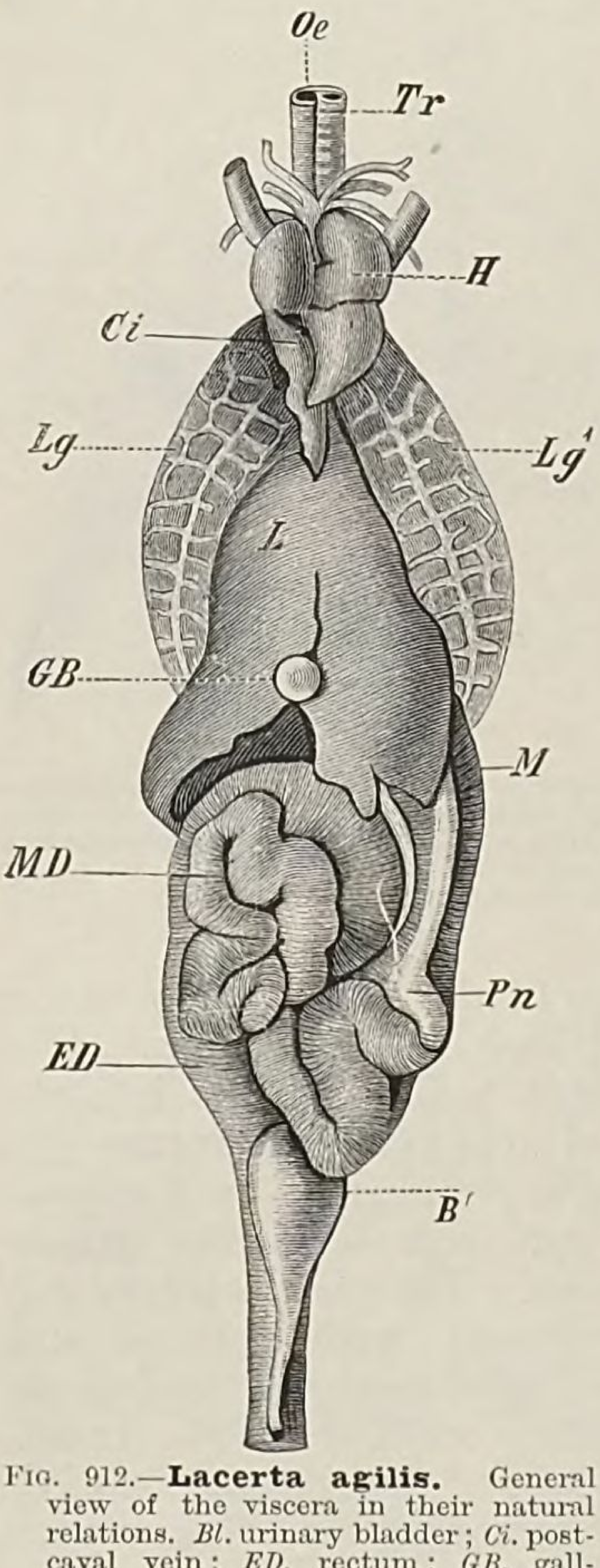


FIG. 912.—**Lacerta agilis.** General view of the viscera in their natural relations. *Bl.* urinary bladder; *Ci.* post-caval vein; *ED*, rectum; *GB.* gall-bladder; *H.* heart; *Lg. Lg'.* the lungs; *M*, stomach; *MD*, small intestine; *Oe.* œsophagus; *Pn.* pancreas; *Tr*, trachea. (After Wiedersheim.)

Digestive system.—The upper and lower jaws, forming the boundary of the aperture of the mouth, are each provided with a single row of small conical teeth, and there is a patch of similar teeth (*palatine teeth*) on the palatine. On the floor of the mouth-cavity is the tongue, a narrow elongated fleshy organ, bifid in front.

The *stomach* (Fig. 912, *M*, Fig. 913, *St*) is a cylindrical organ, but little wider than the œsophagus, and with thick muscular walls. At the point where the small intestine joins the large intestine or rectum, the latter is produced into a short *cæcum* (Fig. 913, *Cæ*). The *liver* (*lr*) is divided into right and left lobes, and a gall-bladder (Fig. 912, *G.B.*; Fig. 913, *g.b.*; Fig. 914, *g.bl*) lies at the lower margin of the right lobe. The *pancreas* (*pn*) is situated in the loop between the stomach and first part of the small intestine or duodenum (*du*). The stomach is attached to the body-wall by a fold of peritoneum, the *mesogaster*, the small intestine by a fold termed the *mesentery*, the rectum by a *meso-rectum*. From the dorsal surface of the liver to the stomach extends a thin fold, the *gastro-hepatic omentum*; and this is continued backwards as the *duodeno-hepatic omentum* connecting the liver with the first portion of the small intestine.

Vascular system.—The *heart* is enclosed, like that of the Frog, in a thin transparent membrane, the *pericardium*. It consists of a *sinus venosus*, *right* and *left auricles*, and an incompletely divided *ventricle*. The *sinus venosus* (Fig. 913, *s. v.*), into which the large

veins open, is thin walled, and has a smooth inner surface. From it a sinu-auricular aperture, guarded by a two-lipped valve, leads

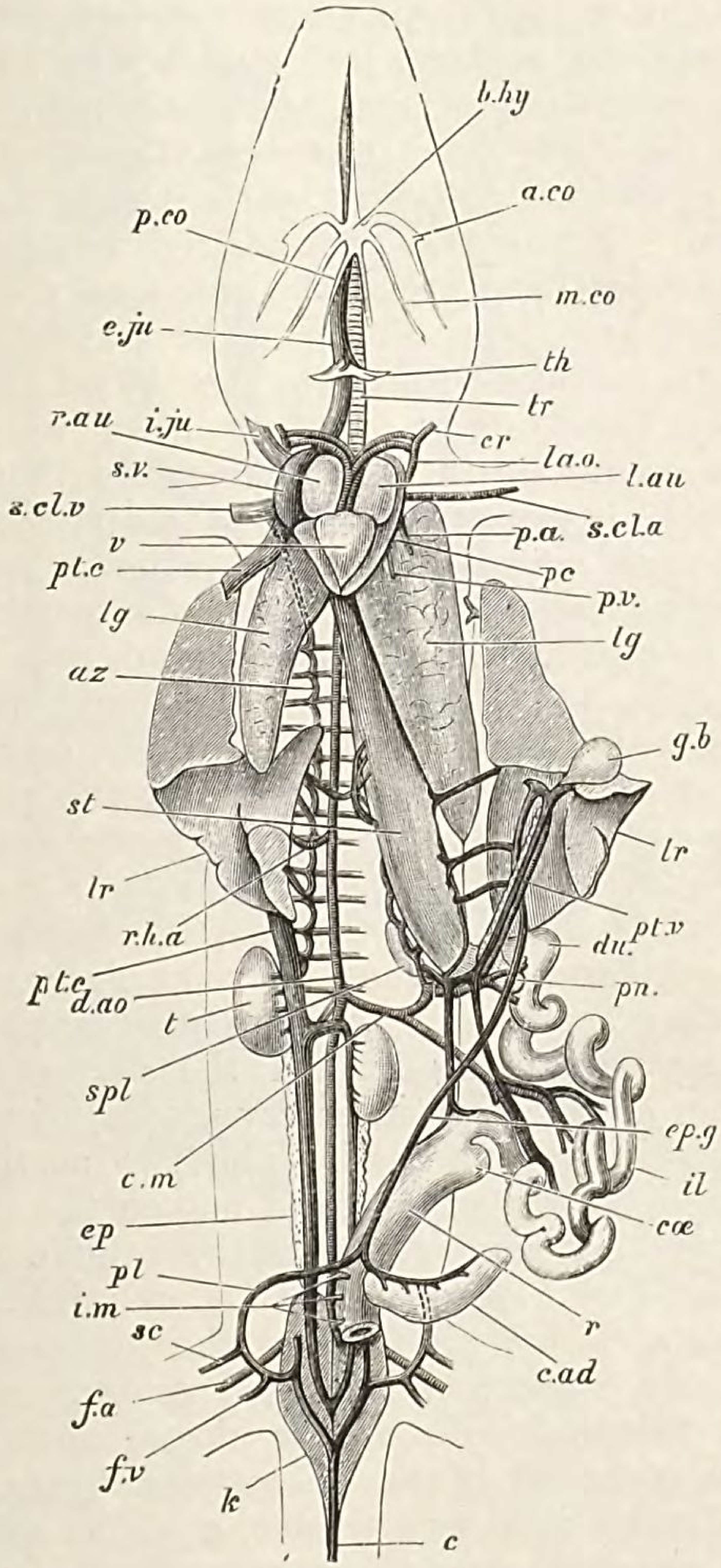


FIG. 913.—**Lacerta viridis.** Dissection from the ventral aspect showing the alimentary, circulatory, respiratory and urinogenital organs (nat. size). The liver (*lr.*) is divided longitudinally and its two halves displaced outwards; the alimentary canal is drawn out to the animal's left; the cloaca with the urinary bladder and posterior ends of the vasa deferentia is removed, as also is the right adipose body. *a. co.* anterior cornu of hyoid; *az.* azygos or cardinal vein; *b. hy.* body of hyoid; *c.* caudal vein; *c. ad.* adipose body; *c. m.* cœliaco-mesenteric artery; *cœ.* cœcum; *cr.* carotid artery; *d. ao.* dorsal aorta; *du.* duodenum; *e. ju.* external jugular vein; *ep.* epididymis; *epg.* epigastric vein; *f. a.* femoral artery; *f. v.* femoral vein; *g. b.* gall-bladder; *i. ju.* internal jugular vein; *il.* ileum; *i. m.* inferior mesenteric arteries; *k.* kidney; *l. ao.* left aortic arch; *l. au.* left auricle; *lg.* lungs; *lr.* liver; *m. co.* middle cornu of hyoid; *p. a.* pulmonary artery; *pc.* pericardium; *p. co.* posterior cornu of hyoid; *pn.* pancreas; *pl.* pelvic vein; *pt. c.* post-caval vein; *pt. v.* portal vein; *p. v.* pulmonary vein; *r.* rectum; *r. au.* right auricle; *r. h. a.* right hepatic artery; *sc.* sciatic vein; *scl. a.* sub-clavian artery; *scl. v.* sub-clavian vein; *spl.* spleen; *st.* stomach; *s. v.* sinus venosus; *th.* thyroid gland; *tr.* trachea; *ts.* testis; *v.* ventricle. (From Parker's *Zootomy.*)

to the right auricle. The *auricles* have their inner surfaces raised up into a network of muscular ridges, the *musculi pectinati.* Both auricles open into the cavity of the ventricle, the aperture of communication, or *auriculo-ventricular aperture*, being divided into two by the auricular septum, and guarded by the auriculo-ventricular valve, consisting of two semi-lunar flaps. The *ventricle* (Fig. 913, *v.*; Fig. 914, *vent.*) has very thick spongy walls, and a small cavity, divided into two parts by an incomplete muscular partition. From the part of the ventricular cavity to the right of the partition arises the pulmonary artery; from the part to the left are given off the right and left aortic arches. When the two auricles contract, the blood from the right auricle (venous blood) tends to run more to the right-hand portion of the cavity of the ventricle, while that from the left auricle (arterial) occupies the left-hand portion. When the ventricle begins to contract its walls come in contact with the dorsal and ventral edges of the ventricular partition, thus completing the separation of the right-hand part of the cavity, containing venous blood, from the left-hand part, containing arterial and mixed blood; and the further contraction results in the driving of the venous blood through the pulmonary artery to the lungs and of the rest through the aortic arches to the head and body. (*Vide* Fig. 945.)

From the right aorta rise the *carotid arteries* (Fig. 913, *cr.*; Fig. 914, *car. art.*), and each runs for some distance parallel with the corresponding aortic arch, with which it anastomoses distally (the connecting part being termed the *ductus Botalli*), having previously given off the carotid artery proper, by means of which the blood is carried to the head. The two aortic arches curve backwards round the œsophagus, the one on the right hand and the other on the left, and meet in the middle line dorsally to form the median *dorsal aorta* (Fig. 913, *d. ao.*; Fig. 914, *dors. aort.*). From the right arch, just in front of the junction, arise the two *subclavian arteries,* right and left, each running outwards to the corresponding fore-limb. From the dorsal aorta the first important branch given off is the *cœliaco-mesenteric* (Fig. 913, *c. m.*). This shortly divides into two trunks, a *cœliac* (Fig. 914, *cœl. a.*) supplying the stomach, spleen, pancreas, duodenum, and left lobe of the liver, and an *anterior mesenteric* supplying the posterior part of the small intestine. Three small *posterior mesenteric* arteries given off further back supply the large intestine. Posteriorly, after giving off *renal* and *genital* branches, and a pair of large *iliacs* to the hind-limb, the dorsal aorta is continued along the tail as the *caudal artery* (Fig. 914, *caud. art.*). Throughout its length, in addition to the larger branches mentioned, the dorsal aorta gives off a regularly arranged series of pairs of small vessels, the *intercostal* and *lumbar* arteries, giving off branches

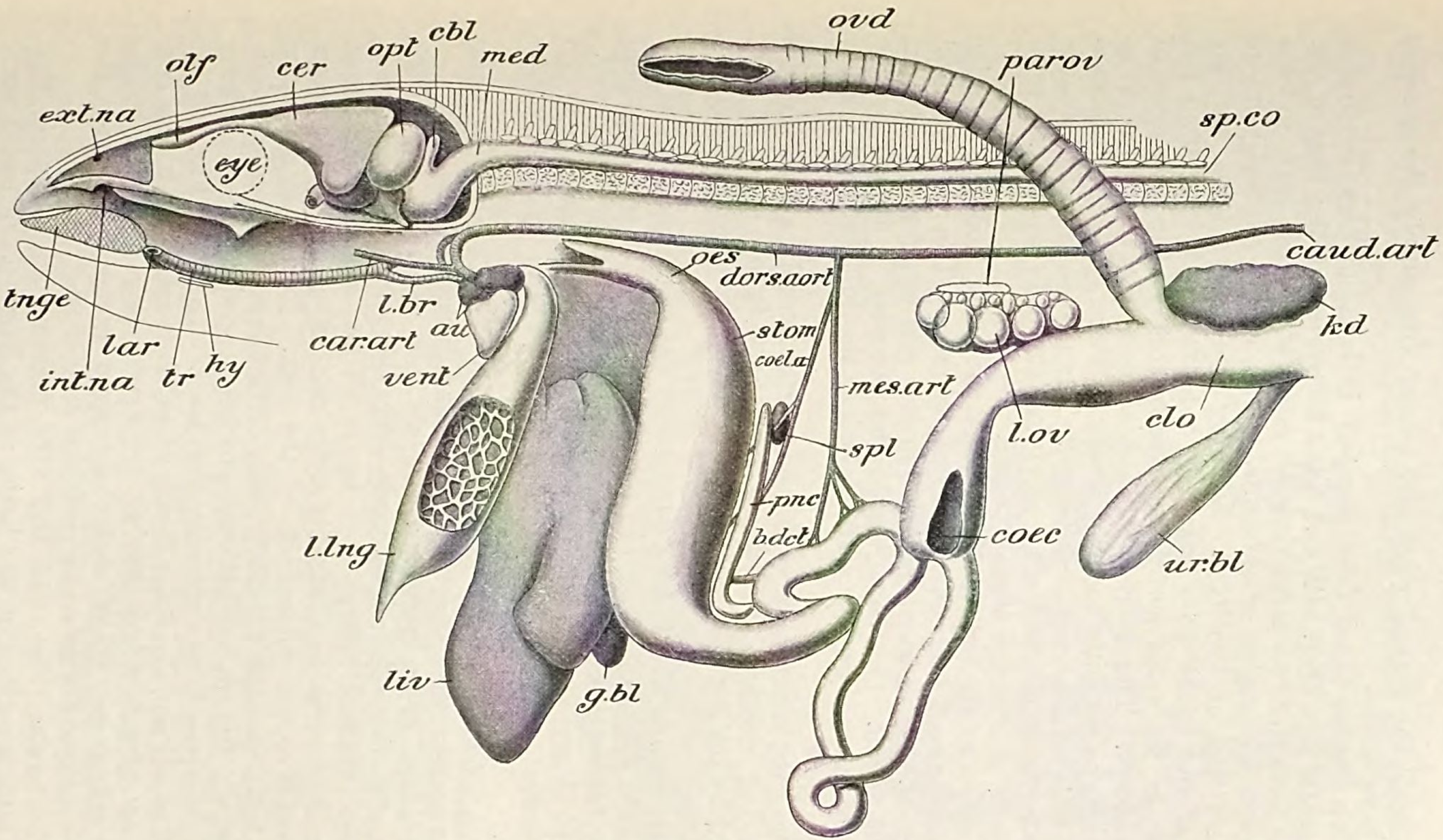


Fig 914.—Lateral dissection of female **Lizard** (semi-diagrammatic). *au.* auricle; *b. dct.* bile-duct; *car. art.* carotid artery; *caud. art.* caudal artery; *cbl.* cerebellum; *cer.* cerebral hemispheres; *clo.* cloaca; *cœc.* cœcum; *cœl. a.* cœliac artery; *dors. aort.* dorsal aorta; *ext. na.* external nares; *eye*, eye; *g. bl.* gall-bladder; *hy.* basi-hyal; *int. na.* internal nares; *kd.* kidney; *lar.* larynx; *l. br.* left bronchus; *liv.* liver; *l. lng.* left lung, opened to show internal structure; *l. ov.* left ovary; *med.* medulla oblongata; *mes. art.* mesenteric artery; *œs.* œsophagus; *olf.* olfactory lobes; *opt.* optic lobes; *ovd.* oviduct (laid aside); *parov.* parovarium; *pnc.* pancreas; *sp. co.* spinal cord; *spl.* spleen; *stom.* stomach; *tnge* tongue; *tr.* trachea; *ur. bl.* urinary bladder; *vent.* ventricle.

that enter the neural canal and others that supply the muscles and integument.

The venous blood from the tail is brought back by means of a *caudal vein* (Fig. 913, *c.*). This bifurcates at the base of the tail to form the two *pelvic* (lateral) *veins* (*pl.*); these unite to form the median *epigastric* or *abdominal* (*ep. g.*), which eventually enters the left lobe of the liver. Entering the pelvic veins are the *femoral* and *sciatic veins* from the hind limb. Arising from the pelvic are the *renal portal veins* distributed to the substance of the kidneys. The *efferent renal veins*, carrying the blood from the kidneys, combine to form a pair of large trunks, which soon unite to form the median *post-caval*. The post-caval runs forwards towards the heart, and, after receiving the wide *hepatic vein* from the liver, enters the sinus venosus.

Two *precavals*, right and left, carry the blood from the anterior extremities and the head to the sinus venosus. The right precaval is formed by the union of the *internal* and *external jugular* and the *subclavian*. On the left side the precaval is formed by the union of *internal jugular* and *subclavian*, the left external jugular being absent.

The liver is supplied, as in other vertebrates, by a *hepatic portal* system of vessels, blood being carried to it by a *portal vein*, formed by the union of gastric, pancreatic, splenic and mesenteric veins.

The *adipose bodies* (Fig. 913, *c. ad.*) are two masses of fat of somewhat semi-lunar shape in the posterior part of the abdominal cavity, between the peritoneum and the muscles of the body-wall.

The *thyroid* is a whitish, transversely elongated body on the ventral wall of the trachea, a short distance in front of the heart.

The *spleen* (Figs. 913 and 914, *spl.*) is a small red body lying in the mesogaster, near the posterior end of the stomach.

Organs of respiration.—A slit-like aperture, the *glottis* situated behind the tongue, leads into a short chamber, the *larynx*, the wall of which is supported by *cricoid* and *arytenoid* cartilages. From the larynx an elongated cylindrical tube, the *trachea*, passes backwards on the ventral side of the neck. Its wall is supported by a large number of small rings of cartilage, the *tracheal rings*. Posteriorly the trachea bifurcates to form two similar but narrower tubes, the *bronchi*, one entering each lung. The *lung* (Fig. 913, *lg.*) is a fusiform sac, the inner lining of which is raised up into a network of delicate ridges, having the appearance of a honeycomb; these ridges are much closer and more numerous towards the anterior than towards the posterior end of the lung.

The **brain** (Figs. 915 and 916) presents all the parts that have been described in the brain of the Frog (p. 263) with some minor modifications. The two cerebral hemispheres (parencephala)

(Fig. 915, *c. h.*) are oval bodies, somewhat narrower in front than behind, closely applied together. Each is prolonged anteriorly into the corresponding *olfactory lobe* (*olf. l.*), a club-shaped process from which the olfactory nerve arises. In the interior of each is a cavity, the *lateral ventricle* or *paracœle*, sending a prolongation forwards into the olfactory lobe, and communicating behind by a small aperture, the *foramen of Monro* (D, *f. m.*), with the diacœle (*v.*3). Through the foramen of Monro there passes into each paracœle a vascular process of pia mater, the *choroid plexus* (*ch. p.*). On the floor of each paracœle is a thickened mass of nerve-matter, the *corpus striatum* (*c.s.*), in front of which passes a transverse band of nerve fibres, the *anterior commissure* (*a. c.*). The *diencephalon* is a small rounded lobe between the paracœles and the mid-brain, and containing a laterally compressed cavity, the *diacœle* (*v.*3). Its roof is extremely thin. Its lateral walls are formed of two thickenings, the *optic thalami*, between which passes across a transverse band, the *posterior commissure* (*p. c.*). Behind the thalami are the

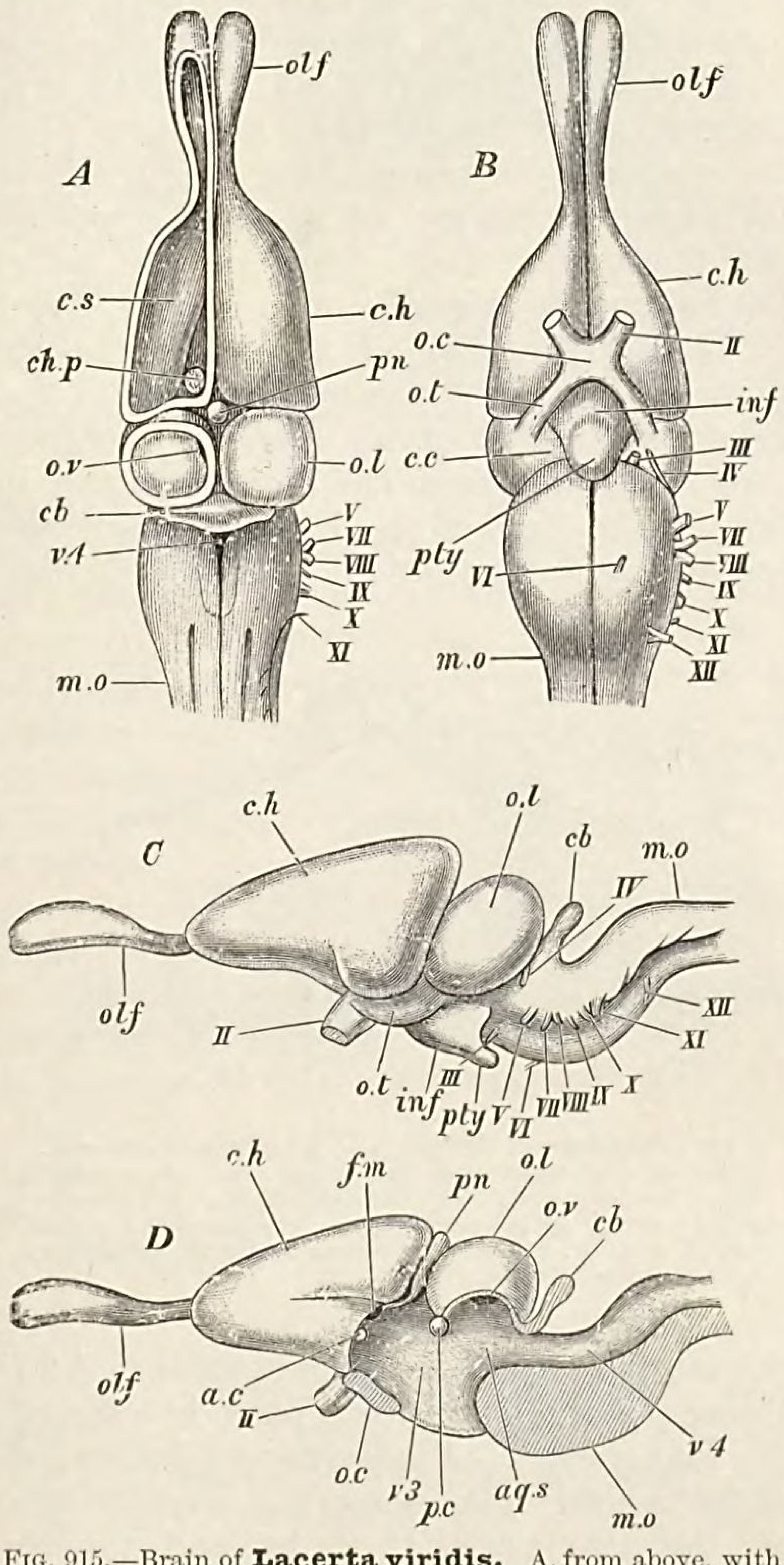


FIG. 915.—Brain of **Lacerta viridis.** A, from above, with the left parencephalon (*c. h.*) and optic lobe (*o. l.*) opened. B, from beneath. C, from the left side. D, in longitudinal vertical section. *a. c.* anterior commissure; *aq. s.* aqueduct of Sylvius; *cb.* cerebellum; *c. c.* crura cerebri; *c. h.* cerebral hemispheres; *ch. p.* choroid plexus; *c. s.* corpus striatum; *f. m.* foramen of Monro; *inf.* infundibulum; *m. o.* medulla oblongata; *o. c.* optic chiasma; *o. l.* optic lobes; *olf.* olfactory lobes; *o. t.* optic tracts; *o. v.* aperture between aqueduct of Sylvius and optic ventricle; *p. c.* posterior commissure; *pn.* pineal body; *pty.* pituitary body; *v*3, diacœle; *v*4, metacœle; I—XII, cranial nerves (From Parker's *Zootomy*.)

optic tracts (*o.t.*) continued into the optic nerves. Behind the optic tracts the floor is produced downwards into a tubular process, the *infundibulum* (*inf.*), ending below in a rounded body, the *pituitary body* or *hypophysis* (*pty.*). The roof is produced into a median process, which is divided into two parts, one corresponding to the epiphysis or pineal body, while the other has connected with its distal extremity an eye-like structure, the *parietal organ* or *pineal eye* (Fig. 916), lying in the parietal foramen. The *mid-brain* consists dorsally of two oval *optic lobes* (*corpora bigemina*) (*o. l.*) and ventrally of a mass of longitudinal nerve-fibres, the *crura cerebri* (*c. c.*), passing forwards to the fore-brain. Each optic lobe contains a cavity (*optocœle*) communicating with a narrow passage leading from the diacœle to the metacœle. The *cerebellum* (*cb.*) is, like that of the Frog, of small size, being a small antero-posteriorly flattened lobe overlapping the anterior portion of the metacœle. The *metencephalon* (medulla oblongata, *m. o.*), broad in front, tapers behind to where it passes into the anterior portion of the spinal cord. The *metacœle* is a shallow space on the dorsal aspect of the medulla oblongata, overlapped in front for a short distance by the cerebellum, and behind covered only by the pia mater, containing a network of vessels, the *choroid plexus* of the metacœle. At the point where medulla oblongata and spinal cord meet is a strong *ventral flexure.*

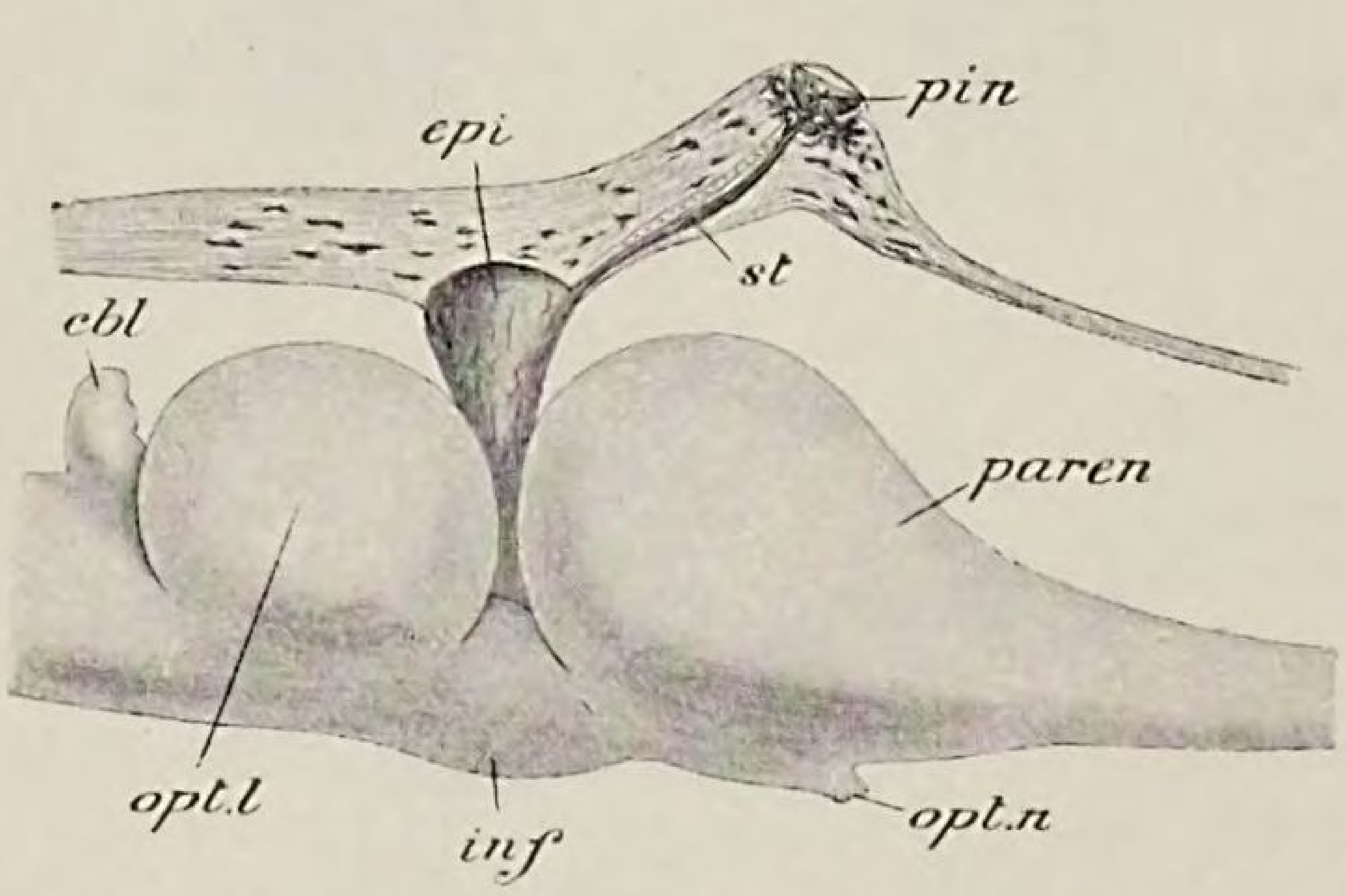


FIG. 916.—Side view of the brain of **Lacerta ocellata,** showing the relations of the pineal eye. *cbl.* cerebellum; *epi.* epiphysis; *inf.* infundibulum; *opt. l.* optic lobes; *opt. n.* optic nerves; *paren.* parencephalon; *pin.* pineal eye; *st.* strand connecting eye with epiphysis. (After Baldwin Spencer.)

The *spinal cord* is continued backwards throughout the length of the neural canal, becoming slightly dilated opposite the origins of the two pairs of limbs, and tapering greatly towards the posterior end of the tail.

The *cranial nerves* resemble those of the Frog as regards their origin and distribution in most respects, the principal difference being that there is intercalated in front of the hypoglossal a *spinal accessory*, and that the hypoglossal arises from the medulla oblongata, not from the spinal cord, and is therefore a cranial nerve

The *nasal cavities* (Fig. 917) open at the extremity of the snout by the external nares, and into the cavity of the mouth by a pair of slit-like internal nares situated near the middle line of the palate.

The external aperture opens into a sort of vestibule, beyond which is the nasal or olfactory cavity proper, containing a convoluted *turbinal bone* over which the mucous membrane extends. Opening into each nasal cavity, near the internal opening, is *Jacobson's organ* (*J. J.*), an oval sac with strongly pigmented walls supported by cartilage.

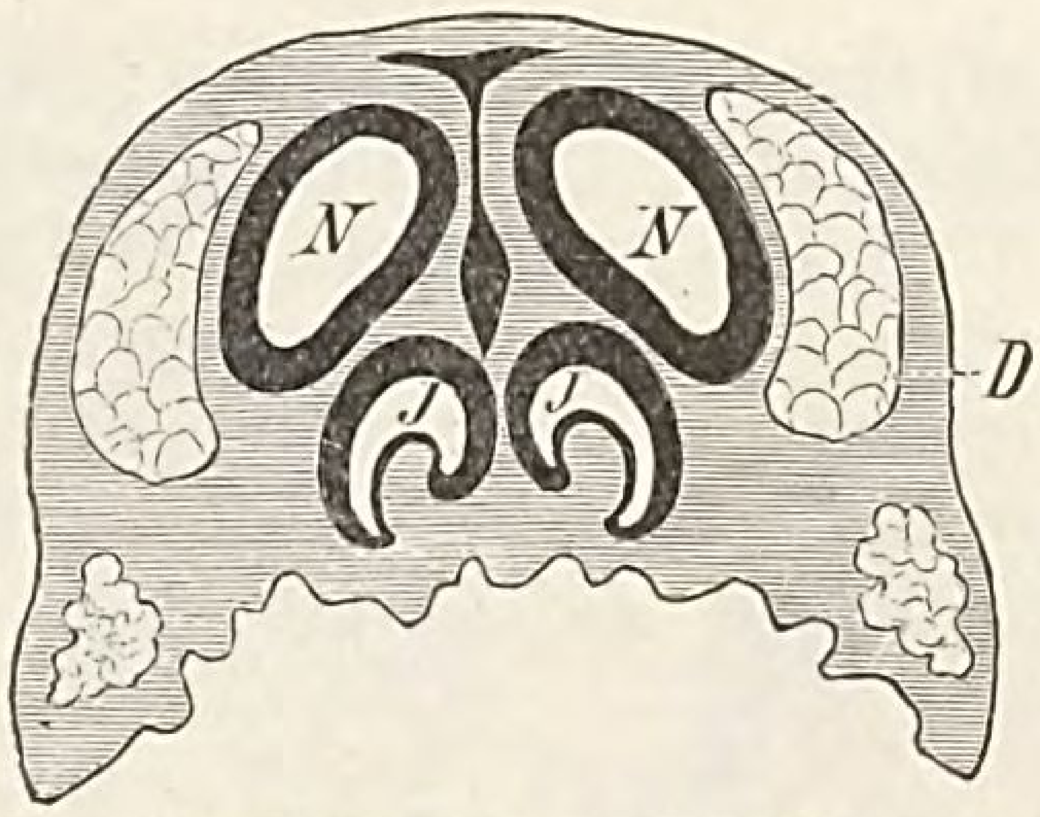


FIG. 917.—Transverse section of the nasal region of the head of **Lacerta** to show the relations of Jacobson's organs. *D*, nasal glands; *J. J.* Jacobson's organs; *N. N.* nasal cavities. (From Wiedersheim's *Comparative Anatomy*.)

The *eye* has a cartilaginous sclerotic having a ring of small bones (Fig. 918) supporting it externally. There is a *pecten* or vascular pigmented process similar to the falciform process in the eye of Teleostomes (p. 199), projecting into the inner chamber of the eye. In essential structure the rest of the eye agrees with that of the Craniata generally as already described. Two glands lie in the orbit, the *lacrymal* and the *Harderian*.



FIG. 918.—Ring of ossicles in sclerotic of eye of **Lacerta.** (After Wiedersheim.)

The *ear* consists of two principal parts, the *middle ear* or *tympanum*, and the *internal ear* or *membranous labyrinth*. The former is closed externally by the tympanic membrane, the position of which has been already mentioned. It communicates with the cavity of the mouth by the Eustachian passage, which is narrower and longer than in the Frog. The inner wall of the tympanic cavity is formed by the bony wall of the auditory region of the skull, in which there are two fenestræ — the *fenestra ovalis* and the *fenestra rotunda*. The columella stretches across the cavity from the tympanic membrane, and is fixed internally into the membrane covering over the fenestra ovalis.

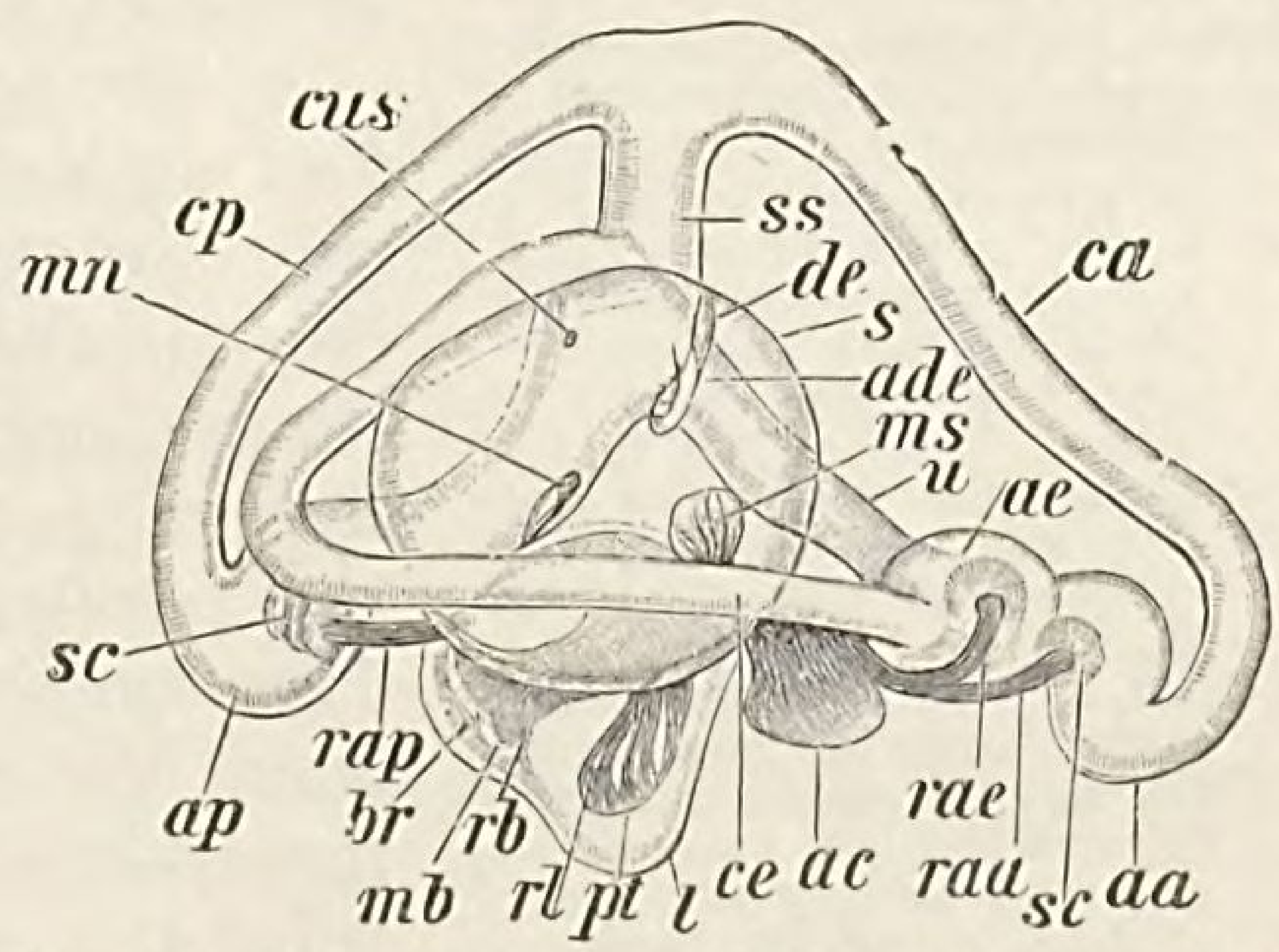


FIG. 919.—Membranous labyrinth of **Lacerta viridis,** viewed from the outer side. *aa.* anterior ampulla; *ac*, auditory nerve; *ade*, opening of the ductus endolymphaticus; *ae*, external ampulla; *ap.* posterior ampulla; *br.* basilar branch of nerve; *ca.* anterior semicircular canal; *ce.* external semicircular canal; *cp.* posterior semicircular canal; *cus.* canal connecting utriculus and sacculus; *de.* ductus endolymphaticus; *l.* lagena; *mb.* basilar membrane; *raa, rae, rap, rl*, branches of auditory nerve; *s.* sacculus; *ss*, common canal of communication between anterior and posterior semicircular canals and utricle; *u.* utriculus. (From Wiedersheim, after Retzius.)

The parts of the membranous labyrinth (Fig. 919) are enclosed by the bones

of the auditory region: between the membranous wall of the labyrinth and the investing bone is a small space containing fluid, the *perilymph*. The labyrinth itself consists of the *utriculus* with the three *semi-circular canals* and the *sacculus* with the *lagena* (*cochlea*). The *utriculus* (*u.*) is a cylindrical tube, bent round at a sharp angle; the *semi-circular canals* (*ca.*, *ce.*, *cp.*) are arranged as in the Frog (p. 265). A narrow tube, the *ductus endolymphaticus*, leads upwards towards the roof of the skull and ends blindly in the dura mater. The *sacculus* is large and rounded. The *lagena* (*l.*) forms a flattened not very prominent lobe, and is of simple form.

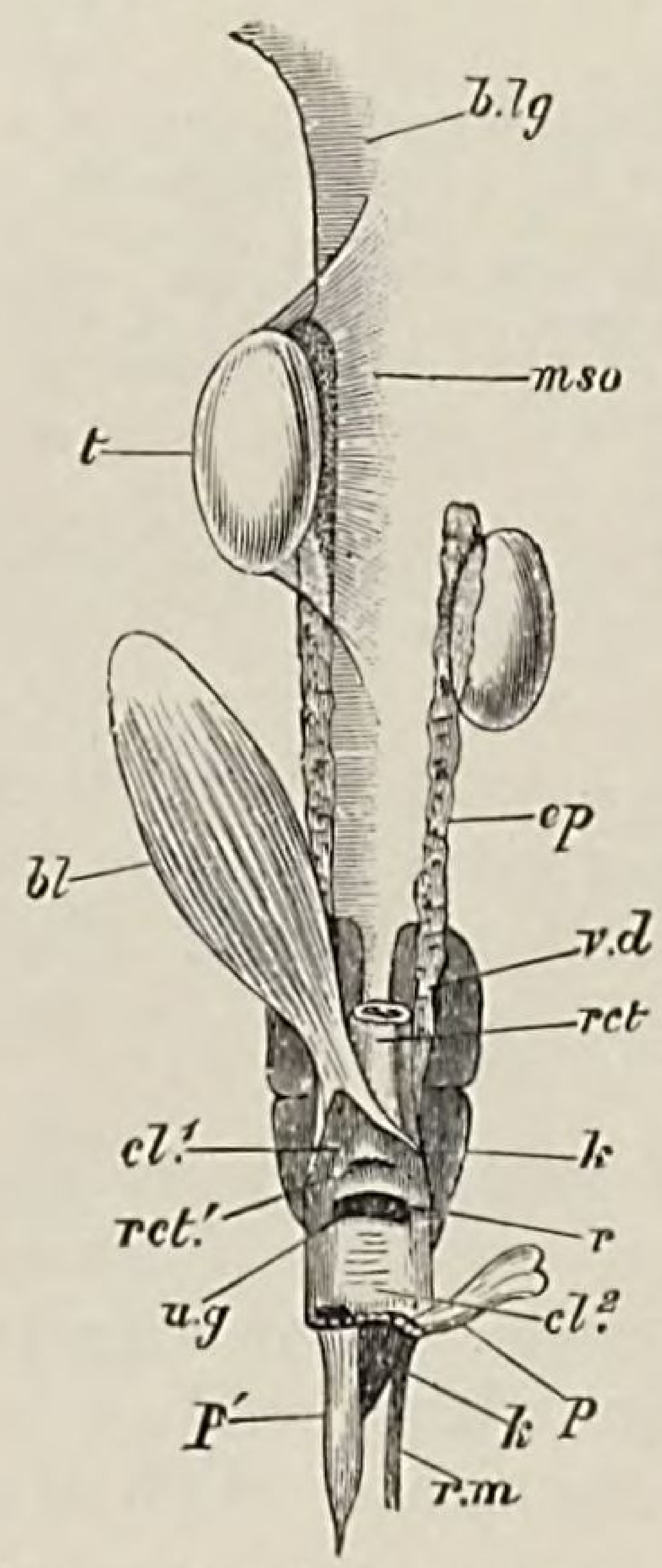


FIG. 920.—Male urinogenital organs of **Lacerta viridis.** The ventral wall of the cloaca is removed, the bladder is turned to the animal's right, and the peritoneal covering of the left testis and epididymis is dissected away. *bl.* urinary bladder; *b.lg*, fold of peritoneum supporting epididymis; *cl.*[1] anterior and *cl.*[2] posterior divisions of the cloaca; *ep.* epididymis; *k.* kidney; *ms. o.* mesorchium; *p*, copulatory organs of which the right is shown retracted (*p'*) and the left everted (*p*); *r. m.* retractor muscle of latter; *r.* ridge separating anterior and posterior divisions of cloaca; *rct.* rectum; *rct.'* its opening into the cloaca; *t.* testis; *u. g.* urinogenital papilla and aperture; *v. d.* vas deferens. (From Parker's *Zootomy*.)

Urinary and Reproductive Systems.—The *kidneys* (Figs. 920 and 921, *k.*) are a pair of irregularly shaped, dark red bodies, each consisting of two lobes, anterior and posterior, situated in close contact with the dorsal wall of the posterior portion of the abdominal cavity, and covered with peritoneum on their ventral faces only. Their posterior portions, which are tapering, are in close contact with one another. Each has a delicate duct, the *ureter*, opening posteriorly into the cloaca. A *urinary bladder* (*bl.*), a thin-walled sac, opens into the cloaca on its ventral side.

In the male the *testes* (Fig. 920, *t.*) are two oval white bodies, that on the right side situated just posterior to the right lobe of the liver, that on the left somewhat further back. Each testis is attached to the body-wall by a fold of the peritoneum, the *mesorchium* (*ms. o.*). The *epididymis* (*ep.*) extends backwards from the inner side of each testis, and passes behind into a narrower convoluted tube, the *vas deferens* or spermiduct (*v. d.*), which opens into the terminal part of the corresponding ureter. A pair of vascular eversible *copulatory sacs* (*p*, *p'*), which when everted are seen to be of cylindrical form with a dilated and bifid apex, open into the posterior part of the cloaca.

In the female the *ovaries* (Fig. 921, *ov.*) are a pair of irregularly oval bodies having their surfaces raised up into rounded elevations,

marking the position of the ova. They are situated a little further back than the testes, and each is attached to the body-wall by a fold of the peritoneum, the *meso-arium* (*ms. o.*). The oviducts (*od.*) are thin-walled, wide, plaited tubes which open in front into the cavity of the body (*od'.*), while behind they open into the posterior part of the cloaca, their opening (*od''.*) being distinct from, and a little in front of, those of the ureters. A fold of the peritoneum, the *broad ligament* (*b. lg.*), attaches the oviduct to the body-wall.

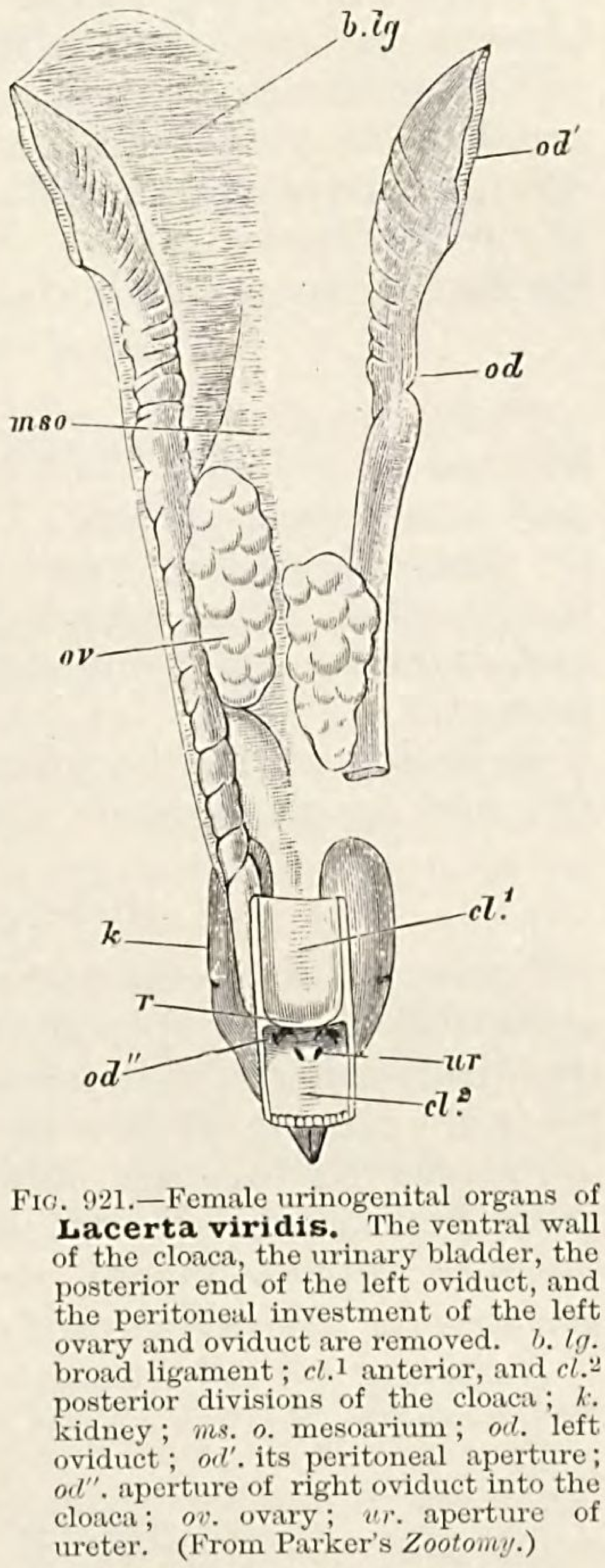


FIG. 921.—Female urinogenital organs of **Lacerta viridis.** The ventral wall of the cloaca, the urinary bladder, the posterior end of the left oviduct, and the peritoneal investment of the left ovary and oviduct are removed. *b. lg.* broad ligament; *cl.*[1] anterior, and *cl.*[2] posterior divisions of the cloaca; *k.* kidney; *ms. o.* mesoarium; *od.* left oviduct; *od'.* its peritoneal aperture; *od''.* aperture of right oviduct into the cloaca; *ov.* ovary; *ur.* aperture of ureter. (From Parker's *Zootomy*.)

2. Distinctive Characters and Classification.

The Reptilia are cold-blooded Craniata with a horny epidermal skeleton of scales, and frequently with an armour of dermal bony plates. The centra of the vertebræ have spheroidal articular surfaces. There are usually only two vertebræ in the sacral region. The episternum, when present, always remains distinct from the clavicles. The floor of the acetabulum is often completely ossified. The pubes and the ischia usually meet in ventral symphyses. The metatarsals do not become ankylosed. The mandible very usually bears teeth. The optic lobes are situated on the dorsal aspect of the brain. The ventricle is rarely divided by a complete partition. There are always two aortic arches in the adult.

Order I.—Squamata.

Reptilia in which the surface is covered with horny epidermal scales, sometimes with the addition of dermal ossifications. The opening of the cloaca is transverse in direction. There is a pair of eversible copulatory sacs in the male. The vertebræ are nearly always procœlous. The sacrum, absent in the Ophidia and Bythonomorpha, consists of two vertebræ in the Lacertilia. The

ribs have simple vertebral extremities. The quadrate is movably articulated with the skull. There is no inferior temporal arch. The nasal apertures of the skull are separate. The limbs, when present, are sometimes adapted for terrestrial locomotion (Lacertilia), sometimes for swimming (Pythonomorpha). The teeth are acrodont or pleurodont (*see below*). The lungs are simple sacs. There is always a wide cleft between the right and left divisions of the ventricular cavity. The optic lobes are approximated, and the cerebellum is extremely small.

Sub-Order a.—Lacertilia.

Squamata in which, as a rule, the limbs are present and are adapted for walking. The mouth is capable of being opened to only a moderate extent. The maxillæ, palatines, and pterygoids are incapable of free movement. The rami of the mandible are firmly united at the symphysis. There are nearly always movable eyelids and a tympanum. A sternum and an episternum are present.

Including all the Lizards, such as the Skincs, Geckos, Monitors, Iguanas, Amphisbænians, Chamæleons, and other groups.

Sub-Order b.—Ophidia.

Squamata with long narrow body, devoid of limbs. The mouth is capable of being opened to form a relatively very wide gape by the divarication of the jaws. The maxillæ, palatines, and pterygoids are capable of free movement. The rami of the mandible are connected together only by elastic fibres at the symphysis, so that they are capable of being widely separated. There is no separate supra-temporal ossification. Sternum and episternum are absent. Movable eyelids and tympanum are absent.

Including all the Snakes—Vipers, Rattlesnakes, Sea-Snakes, Fresh-water Snakes, Tree-Snakes, Blind-Snakes, Pythons, and Boas.

Sub-Order c.—Pythonomorpha.

Extinct Squamata with elongated Snake-like body, provided with limbs which take the form of swimming-paddles. The skull resembles that of the Lacertilia; a supra-temporal helps to suspend the quadrate. The union of the rami of the mandible was ligamentous. There is, as a rule, no sacrum, the ilia not articulating with the spinal column.

ORDER II.—RHYNCHOCEPHALIA.

Lizard-like, scaly Reptiles with well-developed pentadactyle limbs adapted for walking. The opening of the cloaca is transverse. There are no copulatory sacs. The vertebræ are amphicœlous, sometimes enclosing vestiges of the notochord. The

sacrum consists of two vertebræ. Numerous intercentra are usually present. The ribs have simple vertebral extremities, and are provided with uncinates. There is a system of abdominal ribs. The quadrate is immovably fixed to the other bones of the skull. There are both upper and lower temporal arches. The rami of the mandible are united by ligament. There is a sternum. The teeth are acrodont. The lungs, heart, and brain resemble those of the Squamata.

This order comprises only a single living genus, *Hatteria*, together with a number of fossil forms.

Order III.—Chelonia.

Reptilia having the body enclosed in a shell of bony plates, consisting of a dorsal carapace and a ventral plastron, partly of dermal, partly of endoskeletal origin. There is usually on the surface an epidermal exoskeleton of horny plates. The vertebræ and ribs of the thoracic region are firmly fused with the bony carapace, into the composition of which they enter. The quadrate is immovably united with the skull. The nasal apertures in the skull coalesce into one. The limbs are sometimes terminated by clawed digits adapted for terrestrial locomotion, sometimes modified into the shape of flippers. There are no teeth, and the jaws have a horny investment. The lungs are compound sacs. In essentials the heart and brain resemble those of the Squamata. There are no copulatory sacs, but a median penis.

This order includes the Land Tortoises, Soft Tortoises, River and Mud Tortoises, and the Turtles, besides a number of fossil forms.

Order IV.—Theromorpha.

Extinct Reptiles with amphicœlous vertebræ sometimes enclosing remnants of the notochord, with a sacrum composed of from two to six vertebræ, and with ribs having bifid vertebral extremities. There is no sternum. The quadrate is not movable. The limbs are adapted for walking. The pubes and ischia are united. The teeth, which are usually, though not always, present, are highly differentiated and lodged in sockets.

This order comprises a large number of extinct Reptiles, which are grouped in the four sub-orders, Anomodontia, Placodontia, Pareiosauria, and Theriodontia (Fig. 952).

Order V.—Crocodilia.

Reptiles in which the dorsal surface, or both dorsal and ventral surfaces, are covered with rows of sculptured bony scutes. Epidermal scales are also present. The vertebral centra are either amphicœlous, flat at each end, or procœlous. The anterior thoracic

vertebræ have elongated and bifid transverse processes. The sacrum consists of two vertebræ. The ribs are bifid at their vertebral ends. The quadrate is immovable. A sternum is present, and there is a series of abdominal ribs. The limbs are adapted for walking. The teeth are lodged in sockets. The lungs are compound sacs. The ventricle of the heart is completely divided in recent forms. The opening of the cloaca is elongated in the direction of the long axis of the body. There is a median penis.

This order includes among living forms the true Crocodiles, the Gavials, the Alligators, and Caimans.

ORDER VI.—SAUROPTERYGIA.

Extinct aquatic Reptiles with elongated neck, small head, short tail, and usually flipper-like limbs. The centra are slightly amphicœlous or quite flat. The sacrum is composed of two vertebræ. The cervical ribs are bifid, the thoracic simple. The quadrate bone is immovable. There is no sternum. The teeth are situated in sockets (Fig. 953).

ORDER VII.—ICHTHYOPTERYGIA.

Extinct aquatic Reptiles, with large head, without neck, and with elongated tail and completely flipper-like limbs. The centra are amphicœlous, and there is no sacrum. The ribs are bifid at their vertebral ends. The quadrate is immovable. The premaxillæ are drawn out to form an elongated rostrum. There is no sternum, but there is a series of abdominal ribs. The teeth are lodged in a common groove. The integument is naked (Fig. 956).

ORDER VIII.—DINOSAURIA.

Extinct terrestrial Reptiles with elongated limbs, having the surface of the body sometimes naked, sometimes covered with a bony armour. The centra are amphicœlous or opisthocœlous. The sacrum consists of from two to six vertebræ. The ribs are bifid. A sternum is present. The quadrate is fixed. The pelvis usually resembles that of a Bird, the ilium being extended fore and aft, and the pubis, as well as the ischium, directed backwards. The teeth are lodged in sockets, and have compressed crowns (Fig. 957).

ORDER IX.—PTEROSAURIA.

Extinct Reptiles, the structure of which is greatly modified in adaptation to a flying mode of locomotion. The vertebræ are procœlous, the neck elongated. The sacrum contains three or four vertebræ. The anterior thoracic ribs are bifid. The skull resembles

that of a bird in its general shape and in the obliteration of the sutures. There is a ring of sclerotic bones. The quadrate is immovable. There is a sternum. The fore-limbs are modified to act as wings by the great enlargement of the post-axial digit, for the support of a fold of skin. The posterior limbs are weak and have four or five digits. The teeth are implanted in sockets. In the brain the optic lobes were widely separated by the cerebellum, and the latter bore a pair of lateral processes or flocculi (Fig. 959).

Systematic Position of the Example.

There are twenty known species of the genus Lacerta, occurring in Europe, Asia, Africa, and North America. Lacerta is a member of the sub-order Lacertilia of the order Squamata. The flattened and elongated tongue with notched apex places it in the section Leptoglossæ of that sub-order. Among the Leptoglossæ the family Lacertidæ, which comprises Lacerta and a number of other genera, is characterised by the presence of dermal bony supra-orbital and supra-temporal plates, by the presence of small granular or wedge-shaped scales, and of pleurodont conical teeth, excavated at the base. The chief distinctive marks of the genus Lacerta are the presence of comparatively large shields on the head and on the ventral surface, the arrangement of the scales of the trunk in transverse rows which become circular zones or rings on the tail, the development of a collar-like band of larger scales round the neck, and the laterally-compressed falciform claws, grooved on the lower surface.

3. General Organisation of Recent Reptilia.

External Features.—In external form, as in some other respects, certain of the Lacertilia exhibit the least specialised condition to be observed among the living Reptilia. Lacerta is such a central type, and the general account of that Lizard which has just been given applies in all the points of cardinal importance to a large proportion of the Lacertilia. Modifications take place, however, in a variety of different directions. Of such the following are a few of the chief. The tail region is usually, as in the example, extremely long and tapering; but in some groups of Lizards it is comparatively short and thick; and in others it is depressed and expanded into a leaf-like form. In the Chamæleons the long and tapering tail is used as a prehensile organ, the coiling of which round branches of the trees in which the animal lives aids in maintaining the balance of the body in climbing from branch to branch.

In the limbs there is likewise a considerable amount of variation in the different groups of the Lacertilia. Moderately long pentadactyle limbs like those of Lacerta are the rule. In the

Chamæleons both fore- and hind-limbs become prehensile by a special modification in the arrangement and mode of articulation of the digits. In these remarkable arboreal Reptiles the three innermost digits of the manus are joined together throughout their length by a web of skin, and the two outer digits are similarly united: the two sets of digits are so articulated that they can be brought against one another with a grasping movement much analogous to the grasping movements of a Parrot's foot or of the hand of Man. A similar arrangement prevails in the pes, the only difference being that the two innermost and three outermost digits are united. In some groups of Lacertilia, on the other hand, such as the Blind-Worms (*Anguis*), limbs are entirely absent, or are represented only by mere vestiges; and numerous intermediate gradations exist between these and forms, such as Lacerta, with

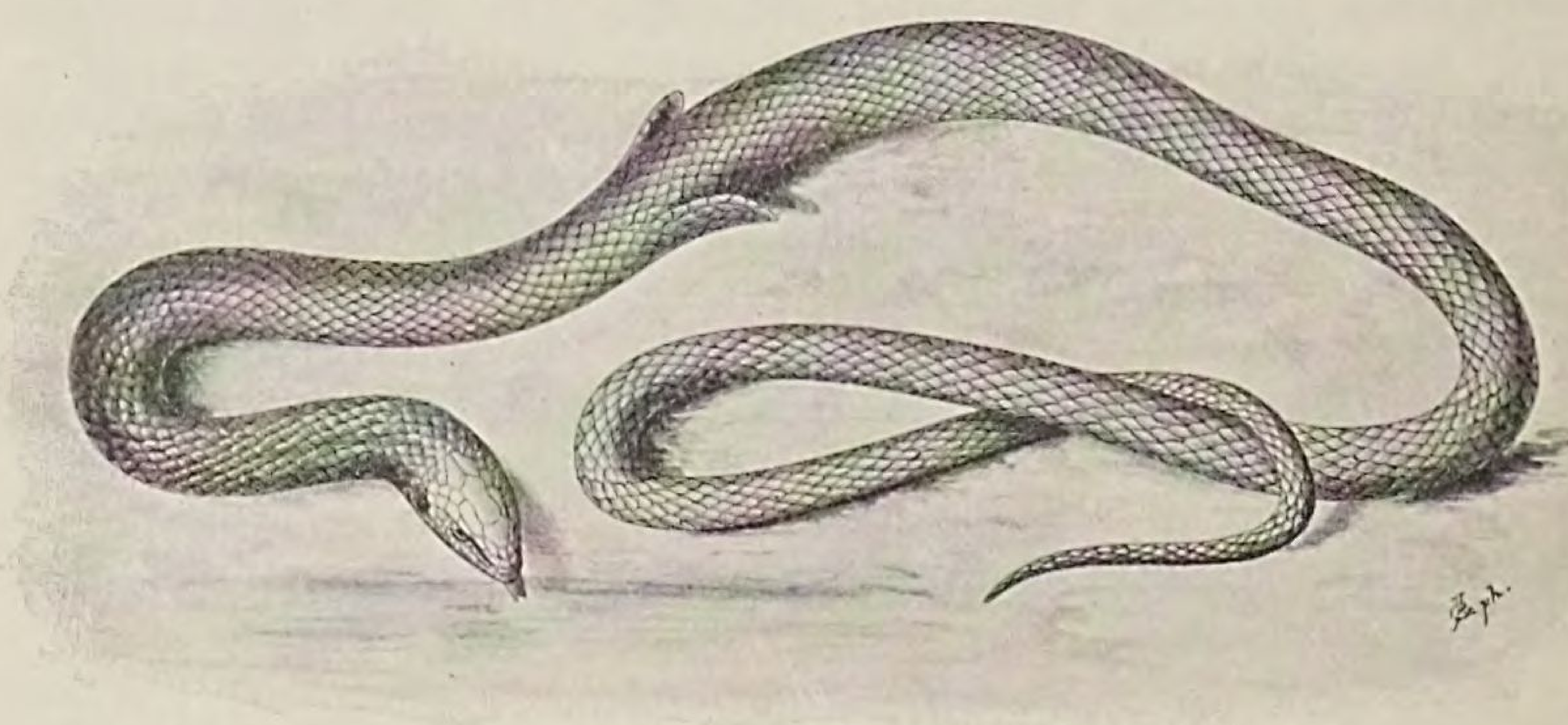


FIG. 922.—**Pygopus lepidopus.** (After Brehm.)

well-developed limbs. The limbless Lizards (Fig. 922) bear a very close resemblance to the Snakes, not only in the absence of the limbs, but also in the general form of the body and the mode of locomotion.

The body of a Snake is elongated, narrow and cylindrical, usually tapering towards the posterior end, sometimes with, more usually without, a constriction behind the head. In the absence of limbs the beginning of the short caudal region is only indicated by the position of the cloacal opening. The fore-limbs are never represented even by vestiges; in some Pythons there are inconspicuous vestiges of hind-limbs in the form of small claw-like processes. The mouth of the Snake is capable of being very widely opened by the free articulation of the lower jaw, and it is this mainly which distinguishes it from the snake-like Lizards. But other, less conspicuous, points of distinction are the absence of movable eyelids in the Snake, and also the absence of a tympanum.

Hatteria, the New Zealand Tuatara (Fig. 923), the only living representative of the Rhynchocephalia, is a Lizard-like Reptile with a well-developed laterally-compressed tail, and pentadactyle ex-

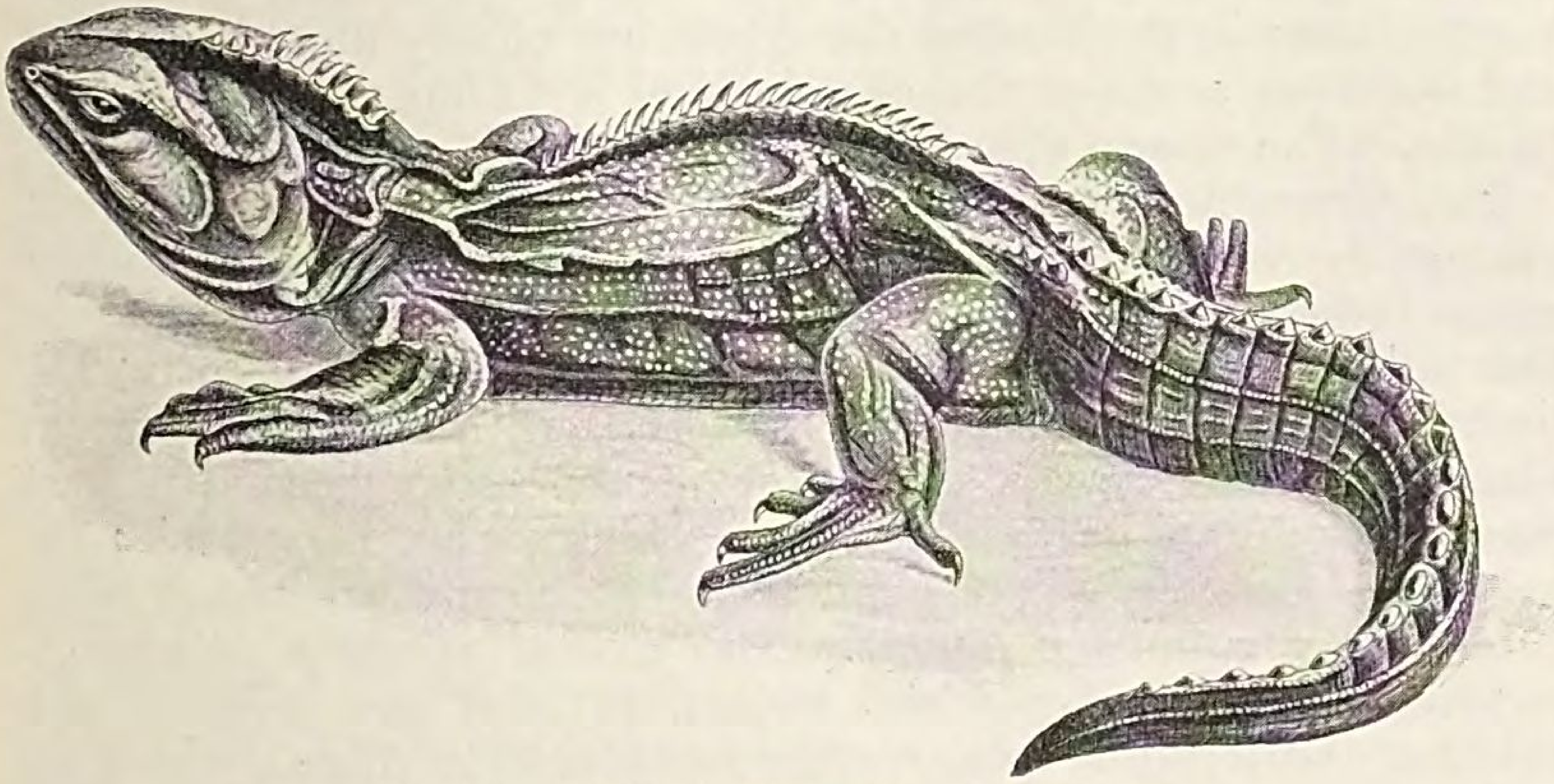


FIG. 923.—**Hatteria punctata.** (After Brehm.)

tremities, very similar to those of a typical Lizard. The upper surface is covered with small granular scales, and a crest of compressed spine-like scales runs along the middle of the dorsal surface. The lower surface is covered with transverse rows of large squarish plates.

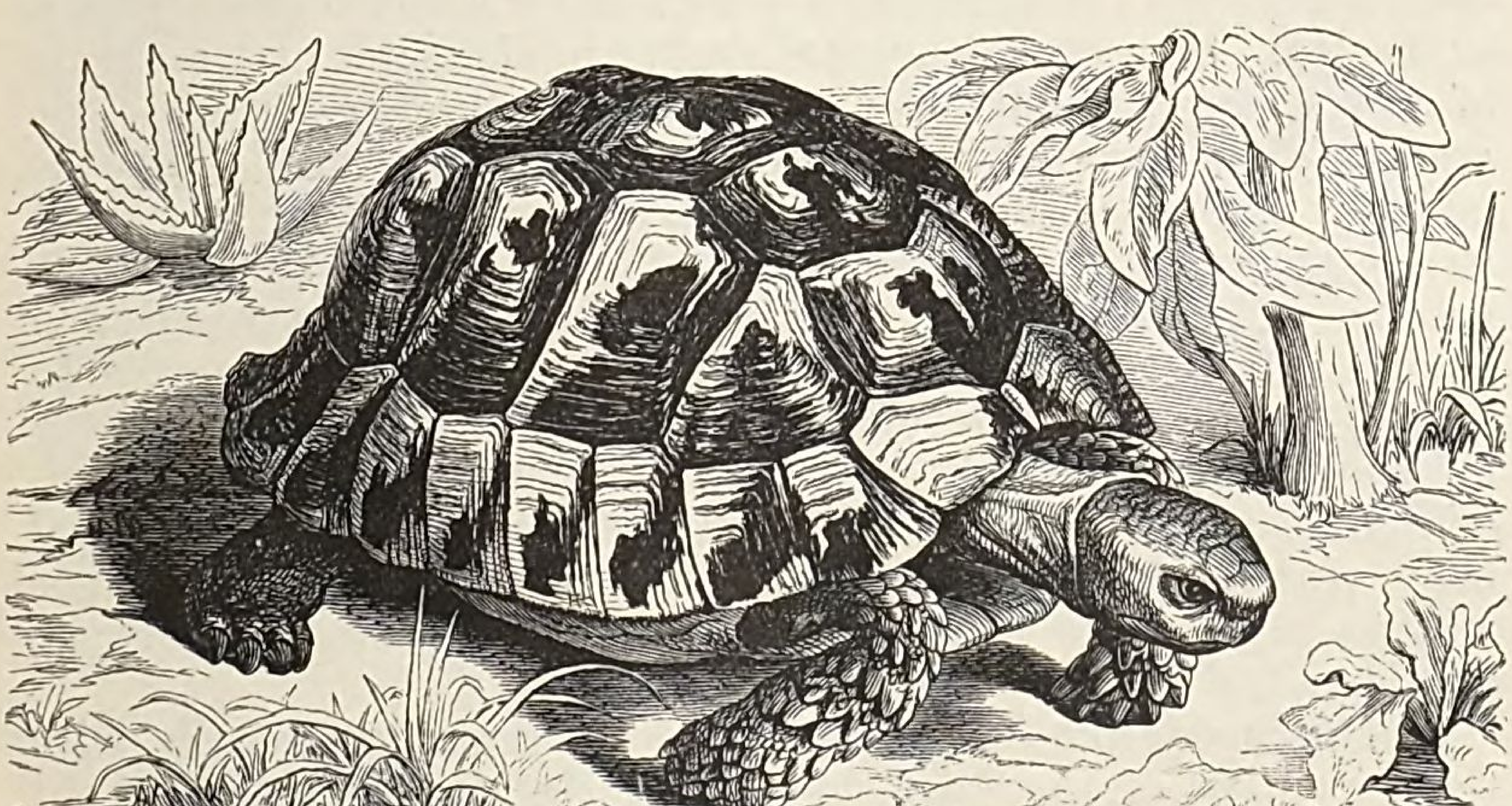


FIG. 924.—Grecian **Tortoise** (Testudo græca). (After Brehm.)

In the Chelonia (Fig. 924) the body is short and broad, enclosed in a hard "shell" consisting of a dorsal part or *carapace* and a ventral part or *plastron*. These are firmly united, apertures being

left between them for the head and neck, the tail and the limbs. The neck is long and mobile; the tail short. The limbs are fully developed though short. In some (land and fresh-water Tortoises) they are provided each with five free digits terminating in curved horny claws; in the Turtles the digits are closely united together, and the limb assumes the character of a "flipper" or swimming paddle. The cloacal aperture is longitudinal.

The Crocodilia, the largest of living Reptiles, have the trunk elongated, and somewhat depressed, so that its breadth is much greater than its height. The snout is prolonged, the neck short, the tail longer than the body and compressed laterally. The limbs are relatively short and powerful, with five digits in the manus and four in the pes, those of the latter being partly or completely united by webs of skin. The eyes are very small; the nostrils placed close to the end of the snout and capable of being closed by a sphincter muscle. The cloacal aperture is a longitudinal slit. The dorsal and ventral surfaces are covered with thick squarish horny plates, often sculptured or ridged, which are supported on bony dermal plates or *scutes* of corresponding form; the horny plates of the dorsal surface of the tail are developed into a longitudinal crest.

Integument and Exoskeleton.—Characteristic of the Squamata is the development in the epidermis of horny plates which cover the entire surface, overlapping one another in an imbricating manner. These differ considerably in form and arrangement in different groups; sometimes they are smooth, sometimes sculptured or keeled. Sometimes they are similar in character over all parts of the surface; usually there are specially developed scales—the *head shields*—covering the upper surface of the head. In the majority of Snakes the ventral surface is covered with a row of large transversely elongated scales, the *ventral shields.* In some Lizards (Chamæleons and Geckos) the scales are reduced and modified into the form of minute tubercles or granules. In some Lizards special developments of the scales occur in the form of large tubercles or spines. Underlying the horny epidermal scales in some Lizards (Skincoids) are a series of dermal bony plates. In the integument of the Geckos are numerous minute hard bodies which are intermediate in character between cartilage and bone.

In the Snake-like Amphisbænians there are no true scales, with the exception of the head shields, but the surface is marked out into annular bands of squarish areas.

In addition to the modification of the scales, the integument of the Chamæleons is remarkable for the changes of colour which it undergoes, these changes being due to the presence in the dermis of pigment cells which contract or expand under the influence of the nervous system, in a way that reminds one of the integument

of the Cephalopoda. Less conspicuous and rapid changes of colour take place in Anguis and in some Snakes.

In the Chelonia, scales, when developed, are confined to the head and neck, the limbs and the tail, but in all of them, with the exception of the Soft Tortoises, both dorsal and ventral surfaces are covered by a system of large horny plates. A series of horny head-shields usually cover the dorsal surface of the head. Beneath the horny plates of the dorsal and ventral surfaces are the bony carapace and plastron, partly composed of dermal bones, but so intimately united with elements derived from the endoskeleton that the entire structure is best described in connection with the latter (*vide infra*).

In the Crocodilia, the dorsal surface is covered with longitudinal rows of sculptured horny plates, beneath which are bony dermal scutes of corresponding form. The ventral surface of the body is covered with scales like those of a Lizard.

A periodical *ecdysis* or casting and renewal of the outer layers of the horny epidermis takes place in all the Reptilia. Sometimes this takes place in a fragmentary manner; but in Snakes and many Lizards the whole comes away as a continuous slough.

Endoskeleton.—The vertebræ are always fully ossified. Only in the Geckos and Hatteria (Fig. 925) are the centra amphicœlous with remnants of the notochord in the inter-central spaces. In most of the others the centra are procœlous, a ball-like convexity on the posterior surface of each centrum projecting into a cup-like concavity on the anterior face of the next. In Hatteria and the Geckos a series of wedge-shaped discs (*intercentra*) are intercalated between the vertebræ of the cervical, part of the thoracic, and caudal regions. The paired bones of the inferior arches (*chevron bones*) are attached to these bones when they are present. In the Lizards in general and the Crocodiles there are inferior processes (*hypapophyses*), perhaps representing intercentra, situated below the centra of the anterior cervical vertebræ. In Chamæleons, Hatteria, and the Crocodiles there is a median bone, the *pro-atlas*, intercalated between the atlas and the occipital region of the skull.



FIG. 925.—Vertebra of **Hatteria**, showing the amphicœlous centrum (*C.*). (After Headley.)

In the Snakes and in Iguanas, in addition to the ordinary articulating processes or zygapophyses, there are peculiar articular surfaces termed *zygosphenes* and *zygantra* (Fig. 926). The zygosphene is a wedge-like process projecting forwards from the anterior face of the neural arch of the vertebra, and fitting, when the vertebræ are in their natural positions, into a depression of corresponding

form—the zygantrum—on the posterior face of the neural arch of the vertebra in front. To this arrangement, as well as to the deeply concavo-convex centra, the extraordinary flexibility and strength of a Snake's backbone are due.

The various regions of the spinal column are well marked in most of the Lizards, in the Chelonia and in the Crocodilia (Fig. 927). In the Snakes and many of the snake-like Lizards only two regions are distinguishable—pre-caudal and caudal. In the others there is a sacral region comprising two vertebræ, all of which have strong transverse processes for articulation with the ilia. The first and second vertebræ are always modified to form an atlas and axis. Ribs are developed in connection with all the vertebræ of the pre-sacral or pre-caudal region; in the caudal region they are usually replaced by inferior arches; but the Chelonia have caudal ribs sometimes fused with the bodies of the vertebræ. In the

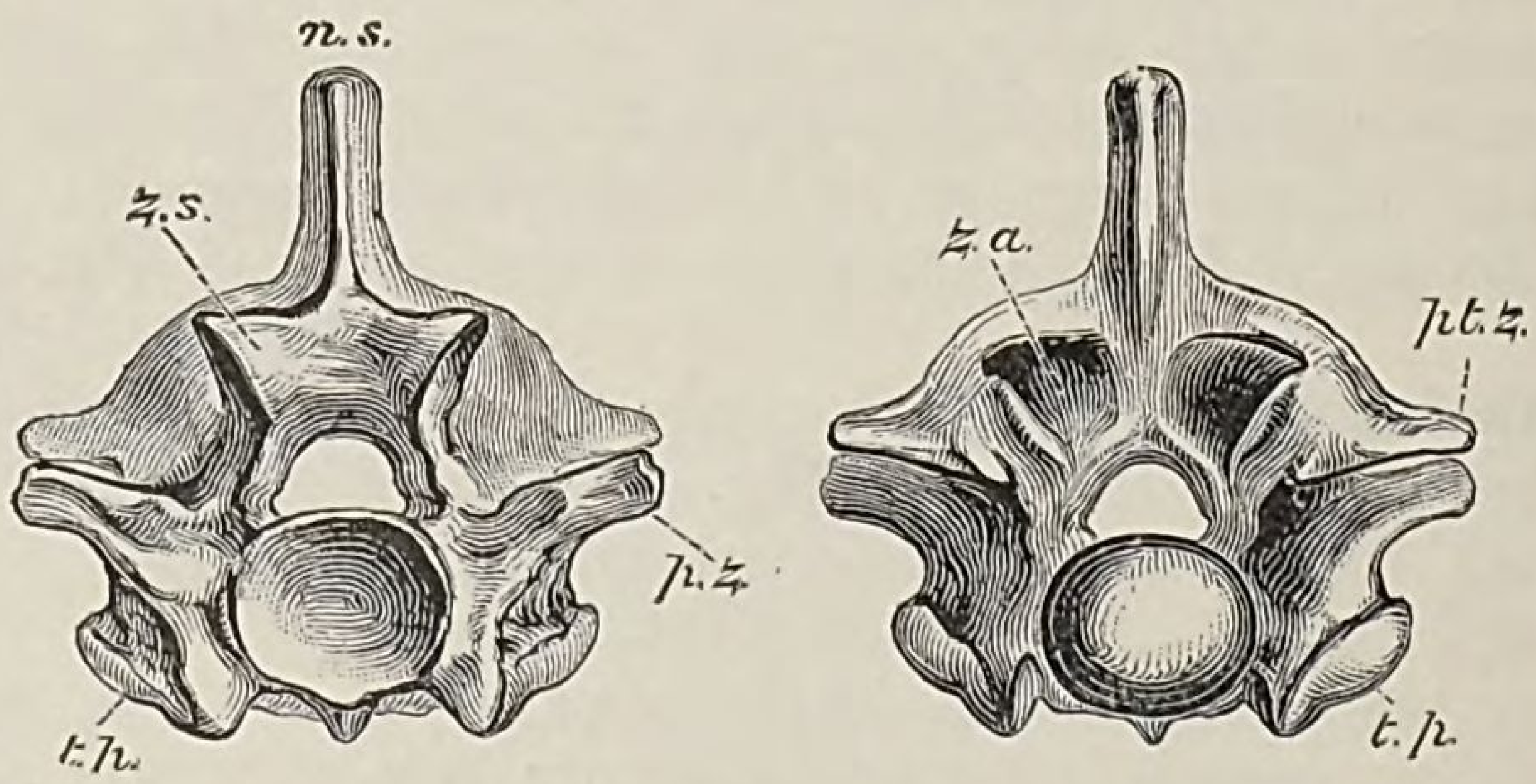


FIG. 926.—Vertebra of **Python**, anterior and posterior views. *n. s.* neural spine; *pt. z.* post; *p. z.* prezygapophyses; *t. p.* transverse processes; *z. a.* zygantrum; *zs.* zygosphene. (After Huxley.)

Lacertilia only a small number (three or four) of the most anterior of the thoracic ribs are connected with the sternum by cartilaginous sternal ribs; the rest are free, or are connected together into continuous hoops across the middle line. In the so-called Flying Lizards (*Draco*) a number of the ribs are greatly produced, and support a pair of wide flaps of skin at the sides of the body, acting as wings, or rather as parachutes. In Hatteria (Fig. 928) and Crocodilia (Fig. 927) each rib has connected with it posteriorly a flattened curved cartilage, the *uncinate*. In the Crocodilia (Fig. 929) there are intercalated between the centra a series of cartilaginous discs, the *intervertebral discs* (*IS*); only three or four ribs are connected with the sternum.

In the Chelonia (Fig. 930) the total number of vertebræ is always smaller than in the members of the other orders. The cervical ribs are small and fused with the vertebræ. The cervical and the caudal are the only regions in which the vertebræ are movable upon one another. The vertebræ of the trunk, usually

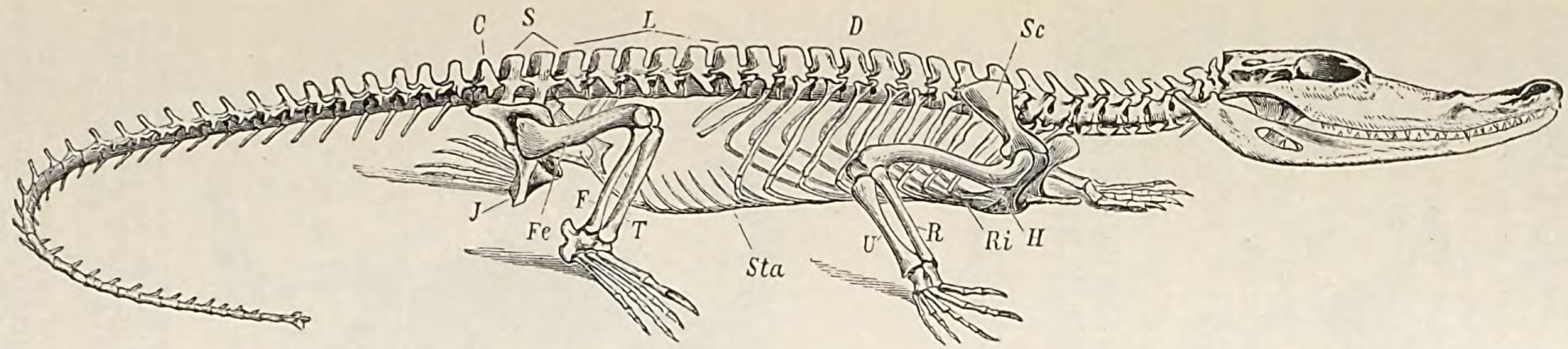


FIG. 927.—Skeleton of **Crocodile.** *C.* caudal region; *D*, thoracic region of spinal column; *F*, fibula; *Fe.* femur; *H.* humerus; *I.* ischium; *L.* lumbar region; *R.* radius; *Ri.* ribs; *S.* sacrum; *Sc.* scapula; *Sta*, abdominal ribs; *T*, tibia; *U.* ulna. (From Zittel.)

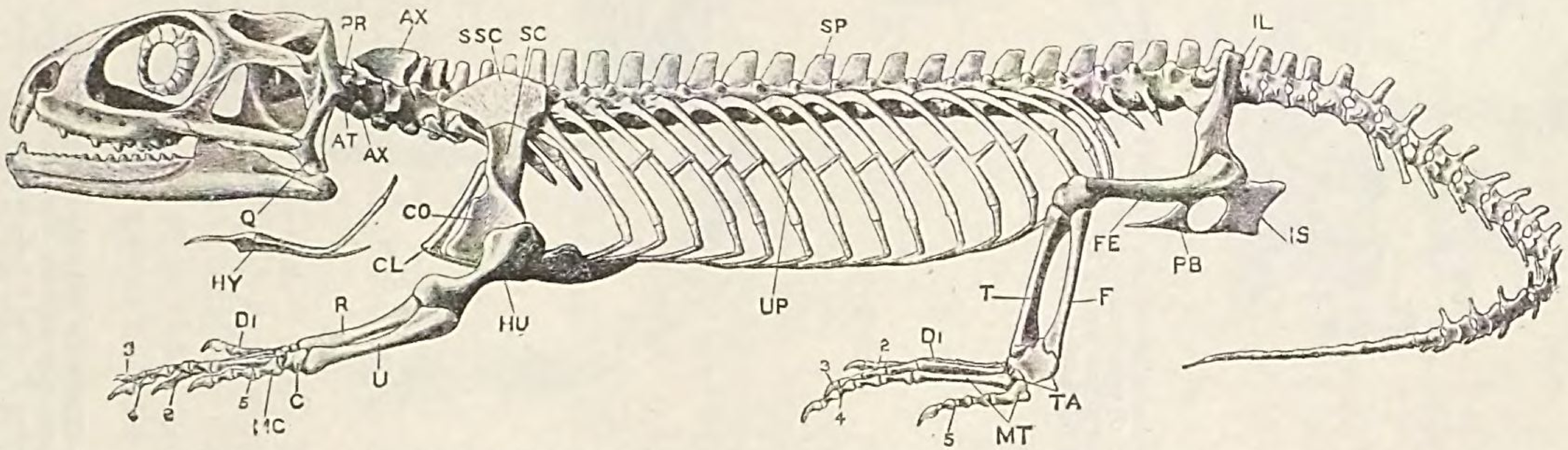


FIG. 928.—Skeleton of **Hatteria.** **AT.** atlas; **AX.** axis; **C.** carpal bones; **CL.** clavicle; **CO.** coracoid; **D.** 1, 2, 3, 4, 5, digits; **FE.** femur; **F.** fibula; **HU.** humerus; **HY.** hyoid; **IL.** ilium; **IS.** ischium; **MC.** metacarpals; **MT.** metatarsals; **PB.** pubis; **PR.** proatlas; **Q.** quadrate; **R.** radius; **SC.** scapula; **SP.** spinal column (points to the spinous processes of one of the thoracic vertebræ); **SSC.** supra-scapula; **T.** tibia; **TA.** tarsals; **U.** ulna; **UP.** uncinate process. (From Headley.)

ten in number, are immovably united with one another by means of fibro-cartilaginous intervertebral discs. Each of the neural

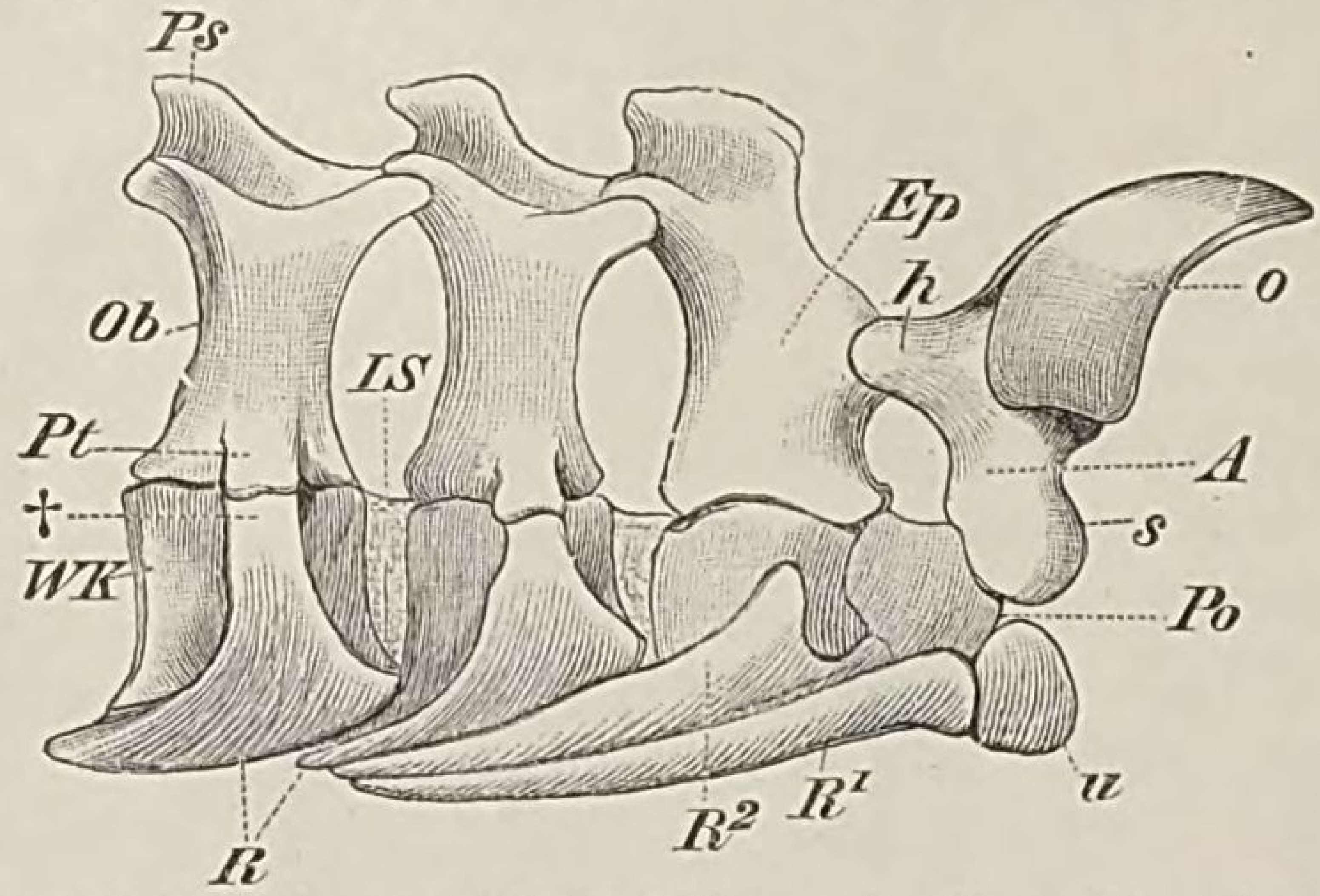


FIG. 929.—Anterior vertebræ of young **Crocodile.** *A.* atlas; *Ep*, axis; *IS*, inter-vertebral discs; *O*, pro-atlas; *Ob*, neural arches; *Po*, odontoid process; *Ps*, spinous processes; *Pt*, transverse processes; *R*. *R*.[1] *R*.[2] ribs; *S*. arch of atlas; *u*. median piece of atlas; *WK*, centra. (From Wiedersheim.)

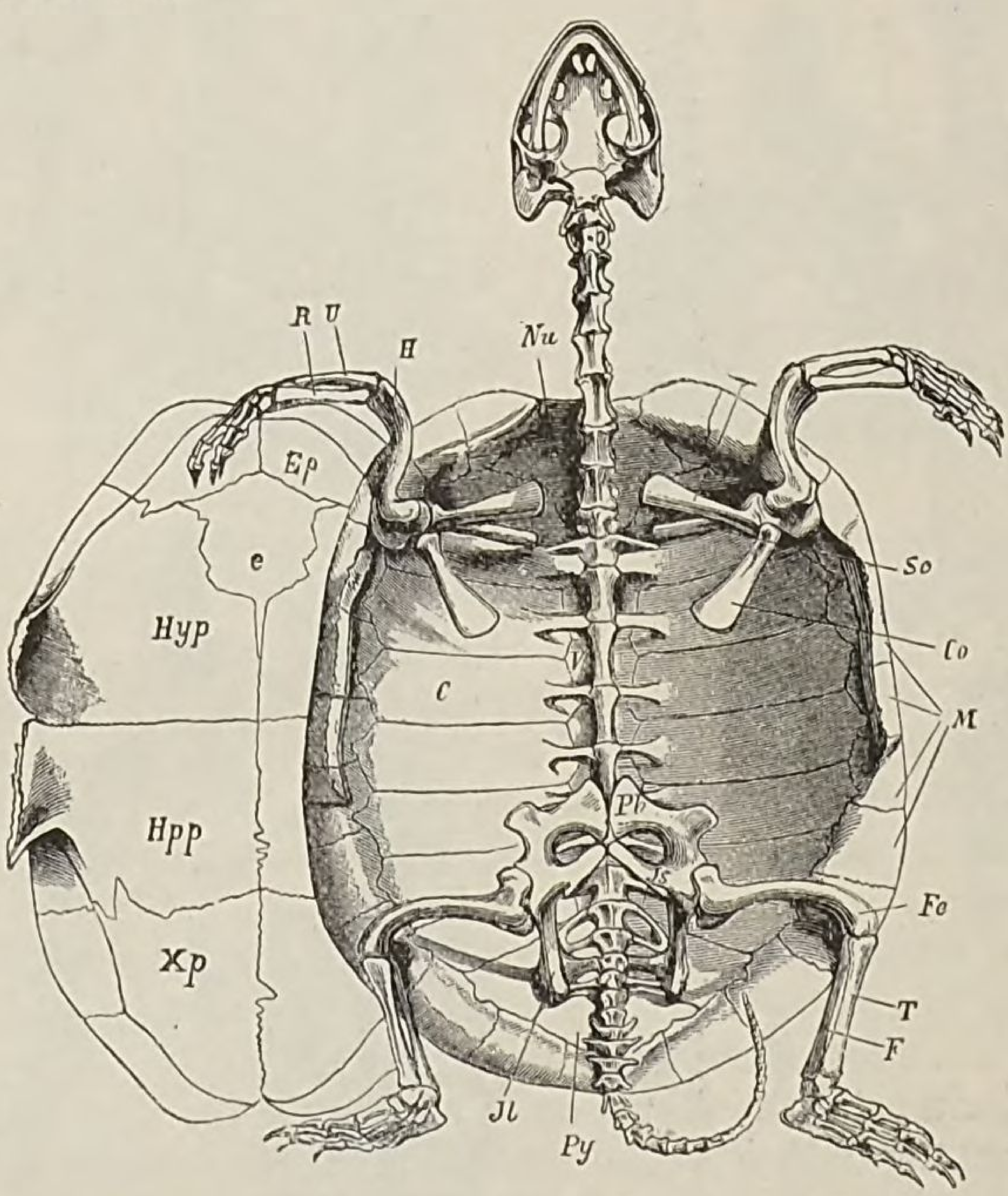


FIG. 930.—**Cistudo lutaria.** Skeleton seen from below; the plastron has been removed and is represented on one side. *C.* costal plate; *Co.* coracoid; *e.* entoplastron; *Ep.* epiplastron; *F.* fibula; *Fe.* femur; *H.* humerus; *Il.* ilium; *Is.* ischium; *M.* marginal plates; *Nu.* nuchal plate; *Pb.* pubis; *Pro.* procoracoid; *Py.* pygal plates; *R.* radius; *Sc.* scapula; *T.* tibia; *U.* ulna. (From Zittel.)

spines, from the second to the ninth inclusively, is expanded into a flat plate, and the row of *neural plates* (Fig. 931, *V*), thus formed, constitutes the median portion of the carapace. The ribs (*R*)

are likewise immovable; a short distance from its origin each passes into a large bony *costal plate* (*C*), and the series of costal plates uniting by their edges form a large part of the carapace on either side of the row of neural plates. The carapace is made up of the neural and costal plates supplemented by a row of *marginal* plates (Figs. 930 and 931, *m*) running along the edge, and *nuchal* (*Nu*) and *pygal* (*Py*) plates situated respectively in front of and behind the row of neural plates.

The bony elements of the plastron of the Chelonia are an anterior and median plate and six pairs of plates—the six pairs probably being of similar nature to the abdominal ribs of the Crocodilia.

The carapace of the Luth or Leather-backed Turtle (*Dermatochelys*) is distinguished from that of the rest of the order in being composed of numerous polygonal discs of bone firmly united together, and in not being connected with the endoskeleton; and in the plastron the median bone is absent.

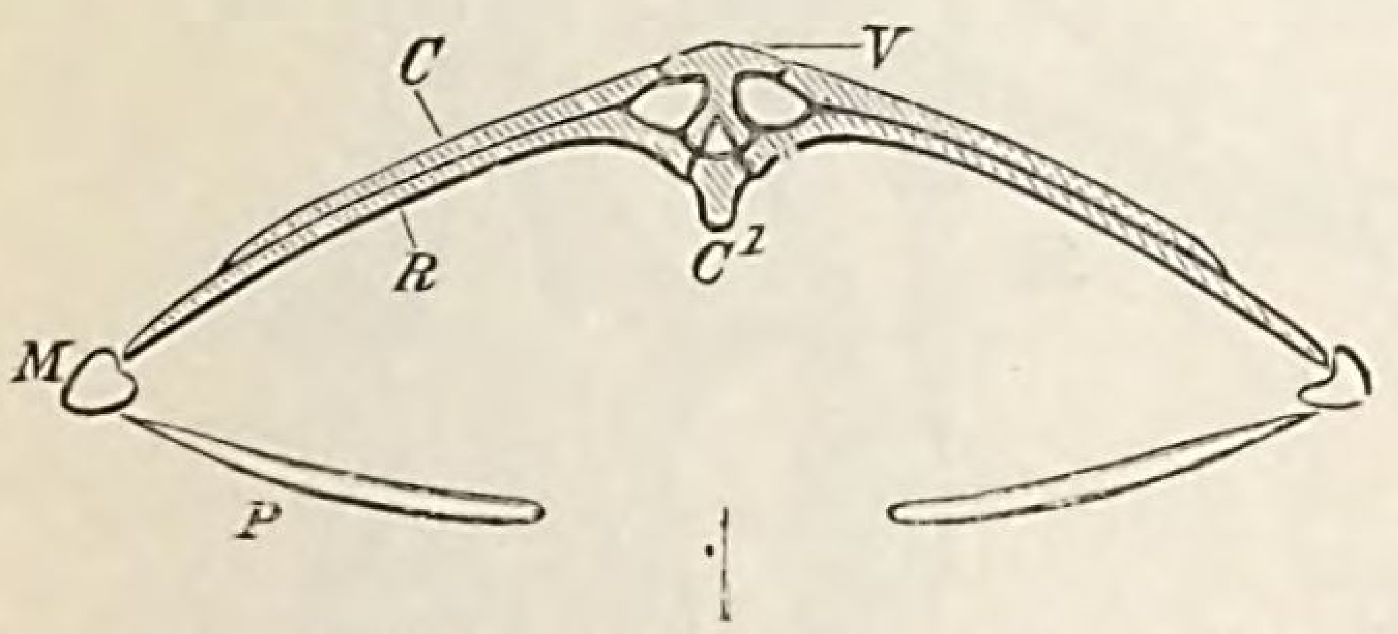


FIG. 931.—**Chelone midas.** Transverse section of skeleton. *C.* costal plate; *C.*[1] centrum; *M.* marginal plate; *P.* lateral element of plastron; *R.* rib; *V.* expanded neural plate. (After Huxley.)

The *sternum* in the Lacertilia is a plate of cartilage with a bifid posterior continuation. In the Ophidia and Chelonia it is absent. In the Crocodilia it is a broad plate with a posterior continuation or *hyposternum*, extending backwards as far as the pelvis.

A series of ossifications—the *abdominal ribs*, with a mesial *abdominal sternum*—lie in the wall of the abdomen in the Crocodilia (Fig. 927, *Sta*), and similar ossifications occur also in the Monitors and in Hatteria. The elements of the plastron of the Chelonia are probably of a similar character.

In the *skull* ossification is much more complete than in the Amphibia, the primary chondrocranium persisting to a considerable extent only in some Lizards and in Hatteria, and the number of bones is much greater. The parasphenoid is reduced, and its place is taken by large basi-occipital, basi-sphenoid, and presphenoid.

A fairly typical Lacertilian skull has been described in the case of Lacerta. Its principal characteristic features are the presence of an inter-orbital septum, the presence of the epipterygoid and the mobility of the quadrate. The last of these features it shares with the Ophidia. The epipterygoid is not universal in the Lacertilia, being absent in the Geckos, the Amphisbænians, and the Chamæleons. The skull of the Chamæleons has a remarkable helmet-

like appearance owing to the development of processes of the squamosal and occipital regions, which unite above the posterior part of the cranial roof. The skull of the Amphisbænians differs from that of other Lacertilia and approaches that of Snakes in the absence of an inter-orbital septum.

In the skull of the Ophidia (Fig. 932) orbito-sphenoidal and alisphenoidal elements are absent, their places being taken by downward prolongations of the parietals and frontals. In the

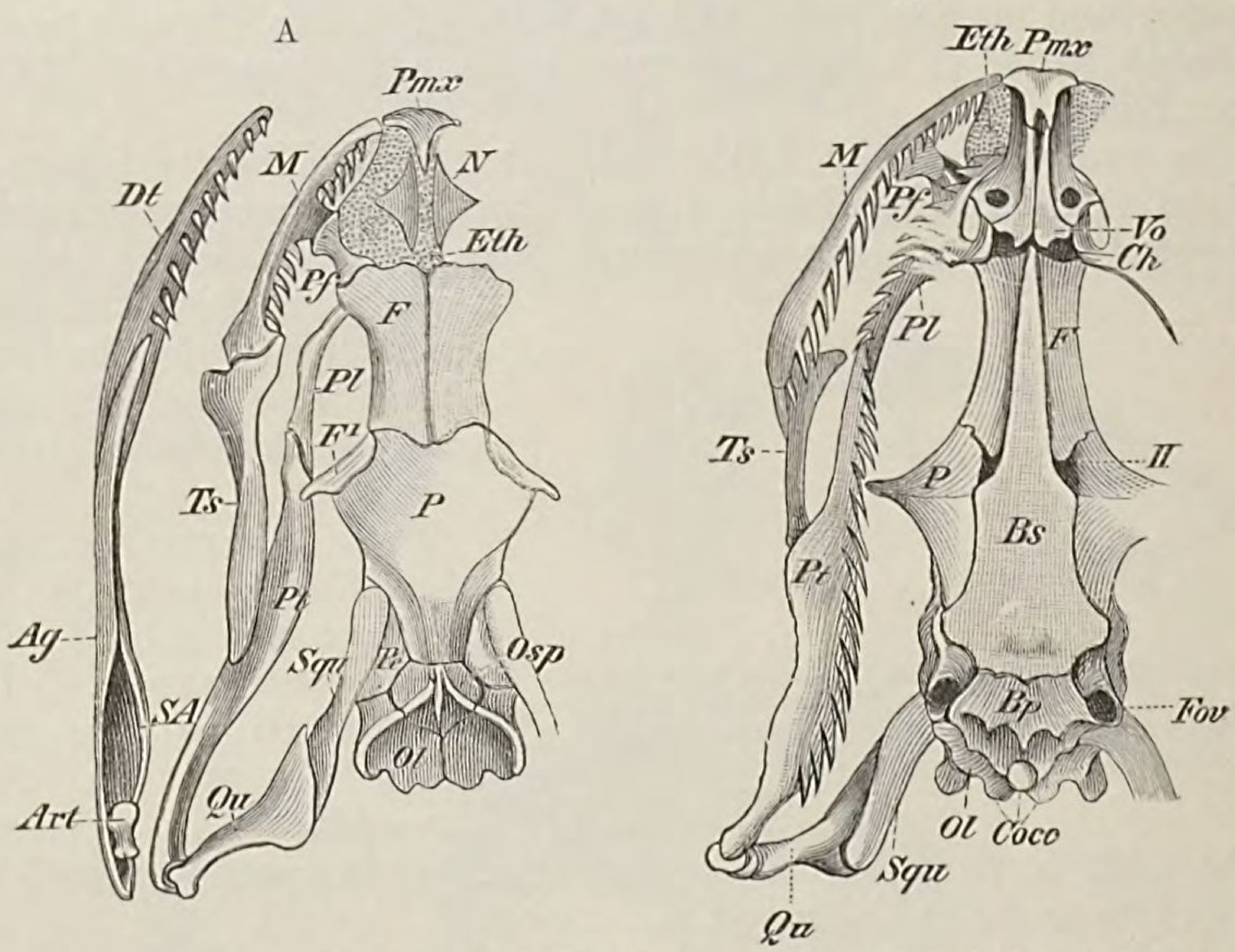


FIG. 932 —Skull of Colubrine Snake (**Tropidonotus natrix**). A, from below; B, from above. *Ag.* angular; *Art.* articular; *Bp.* basi-occipital; *Bs.* basisphenoid; *Ch*, internal nares; *Cocc.* occipital condyle; *Dt.* dentary; *Eth.* ethmoid; *F*, frontal; *F'*, post-orbital; *F. ov.* Fenestra ovalis; *F. p.* parietal foramen; *Jug.* jugal; *M.* maxilla; *N.* nasal; *Osp.* supra-occipital taking the place of orbito-sphenoid; *P.* parietal; *Pe.* prootic; *P. f.* pre-frontal; *Pl.* palatine; *Pmx.* pre-maxilla; *Pt.* pterygoid; *Ol.* exoccipital; *Qu.* quadrate; *SA.* supra-angular; *Squ.* squamosal; *Ts.* transverse; *Vo.* vomer; *II*, optic foramen. (After Wiedersheim.)

substance of the mesethmoid are two cartilaginous tracts (Fig. 933, B, *T*) which are the persistent trabeculæ of the fœtal skull. The inter-orbital septum is absent, and the cranial cavity is prolonged forwards to the ethmoidal region. The palatines (*Pl*) are movably articulated with the base of the skull; as in the Lizards they are widely separated from one another, and do not develop palatine plates. They are movably articulated behind with the pterygoids (*Pt*), and, through the intermediation of the slender transverse bones (*Ts*), with the maxillæ. The pre-maxillæ are very small (in some venomous Snakes entirely absent), and when present usually fused together. The maxillæ (*Mx*), usually short, articulate by means of a movable hinge-point with

the lacrymal (*La*), which, in turn, is movably connected with the frontal. The long and slender quadrate (*Qu*) is freely articulated with the posterior end of the elongated squamosal. The rami of the mandible, likewise long and slender, are not united anteriorly in a symphysis, but are connected together merely by elastic ligamentous tissue, so that, when the mouth of the Snake is opened to allow of the entry of the relatively large prey, which it swallows whole, they are capable of being widely separated from one another. The Typhlopidæ differ from the rest of the Ophidia in having the maxillæ immobile, the quadrate more closely connected with the

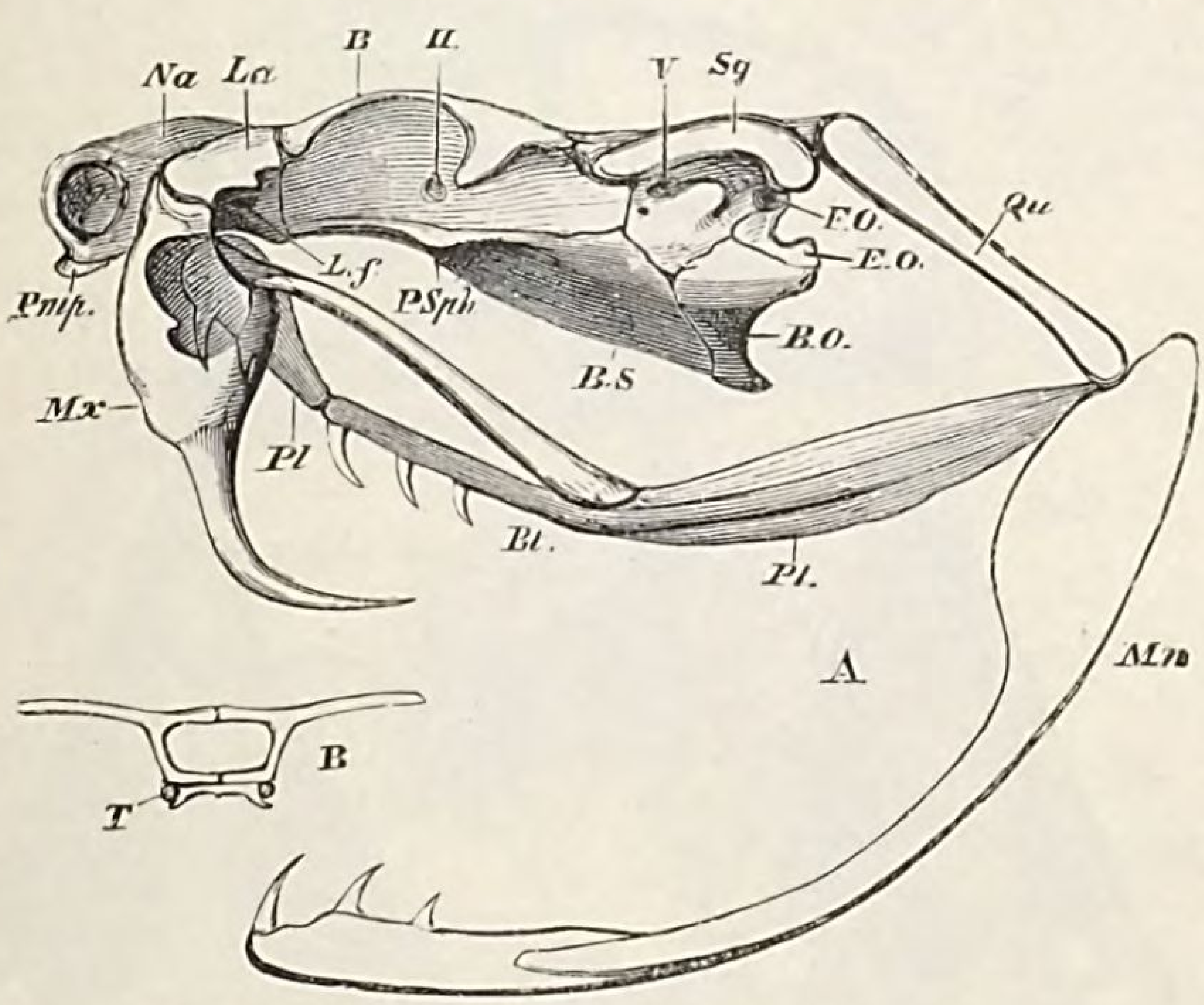


FIG. 933.—A, lateral view of skull of **Rattlesnake (Crotalus).** *B. O.* basi-occipital; *B. S* basi-sphenoid; *E. O.* exoccipital; *F. O.* fossa-ovalis; *La* conjoined lacrymal and pre-frontal; *L. f.* articulation between lacrymal and frontal; *Mn.* mandible; *Mx.* maxilla; *Na.* nasal; *Pl.* palatine; *Pmx.* pre-maxilla; *P. Sph.* pre-sphenoid; *Pt.* pterygoid; *Qu.* quadrate; *Sq.* squamosal; *II, V,* foramina of exit of the second and fifth cranial nervsə; B, transverse section at point lettered B in Fig. A; *T.* trabeculæ. (After Huxley.)

skull, and the rami of the mandible united by a fibro-cartilaginous symphysis.

The skull of Hatteria (Fig. 934) differs from that of the Lizard mainly in the following points. There is a large *superior temporal fossa* bounded by the parietal, post-orbital (*P. or*), and squamosal, and separated below by a bar of bone (*superior temporal arch*) formed of processes of the last two bones from a still larger space—the *lateral temporal fossa.* The latter is bounded below by a slender bony bar (the *inferior temporal arch*), formed of the long narrow jugal (*Ju*), with a small quadrato-jugal, by which the jugal is connected with the quadrate. The quadrate (*Qu*) is immovably fixed, wedged in by the quadrato-jugal, squamosal, and pterygoid. The pre-maxillæ (*Pmx*) are not fused together, but separated by a suture.

In the Chelonia (Figs. 935, 936) all the bones, including the quadrate, are solidly connected together. There is an inter-

orbital septum (Fig. 935, *Si*). The posterior part of the skull has, in the Turtles (Fig. 936, *A*), a false roof formed by upgrowths of the occipital, parietal, and squamosal. The palatines (*pal*) are approximated, and develop palatine plates which for a short distance cut off a nasal passage from the cavity of the mouth. The rami of the mandibles are stout, and are firmly united together at the symphysis.

In the Crocodiles (Fig. 937), as in the Chelonia, the quadrate (*Qu*) is firmly united with the other bones of the skull. There is a

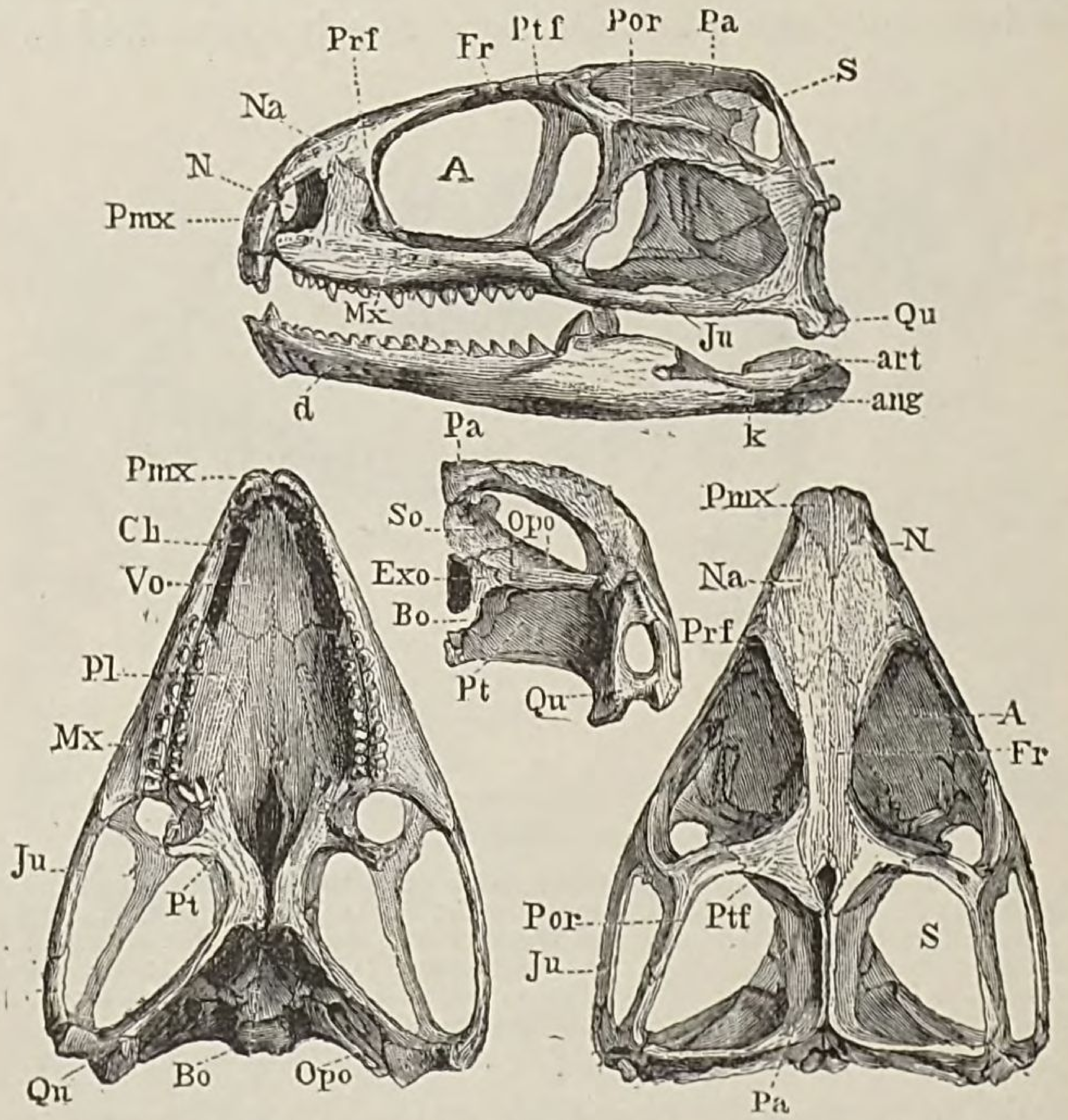


FIG. 934.—Skull of **Hatteria,** viewed from the side (upper figure); from below (lower left-hand figure); from above (lower right-hand figure); and from behind (central figure). *A*, orbits; *ang.* angular; *art.* articular; *Bo.* basi-occipital; *Ch*, internal nares; *d.* dentary; *Exo.* ex-occipital; *Fr.* frontal; *Ju.* jugal; *mx.* maxilla; *N.* external nares; *Na.* nasal; *Op. o.* opisthotic; *Pa.* parietal; *P. mx.* pre-maxilla; *P. or* Post-orbital; *Prf.* pre-frontal; *Pt. f.* post-frontal; *Qu.* quadrate; *Qu. J.* quadrato-jugal; *So.* supra-occipital; *Sph*, basi-sphenoid; *Sq.* squamosal; *Vo.* vomer. (After Zittel.)

membranous and cartilaginous inter-orbital septum. Both palatine (*Pl*) and pterygoid (*Pt*) as well as maxillæ, develop palatine plates in the roof the mouth, cutting off a nasal passage of great length from the cavity of the mouth, the posterior nares (*ch*) being situated far back towards the posterior end of the cranial base. The nature of the articulation between the mandible and the quadrate is such that movement is restricted to the vertical plane, and lateral displacement is further provided against by the development of

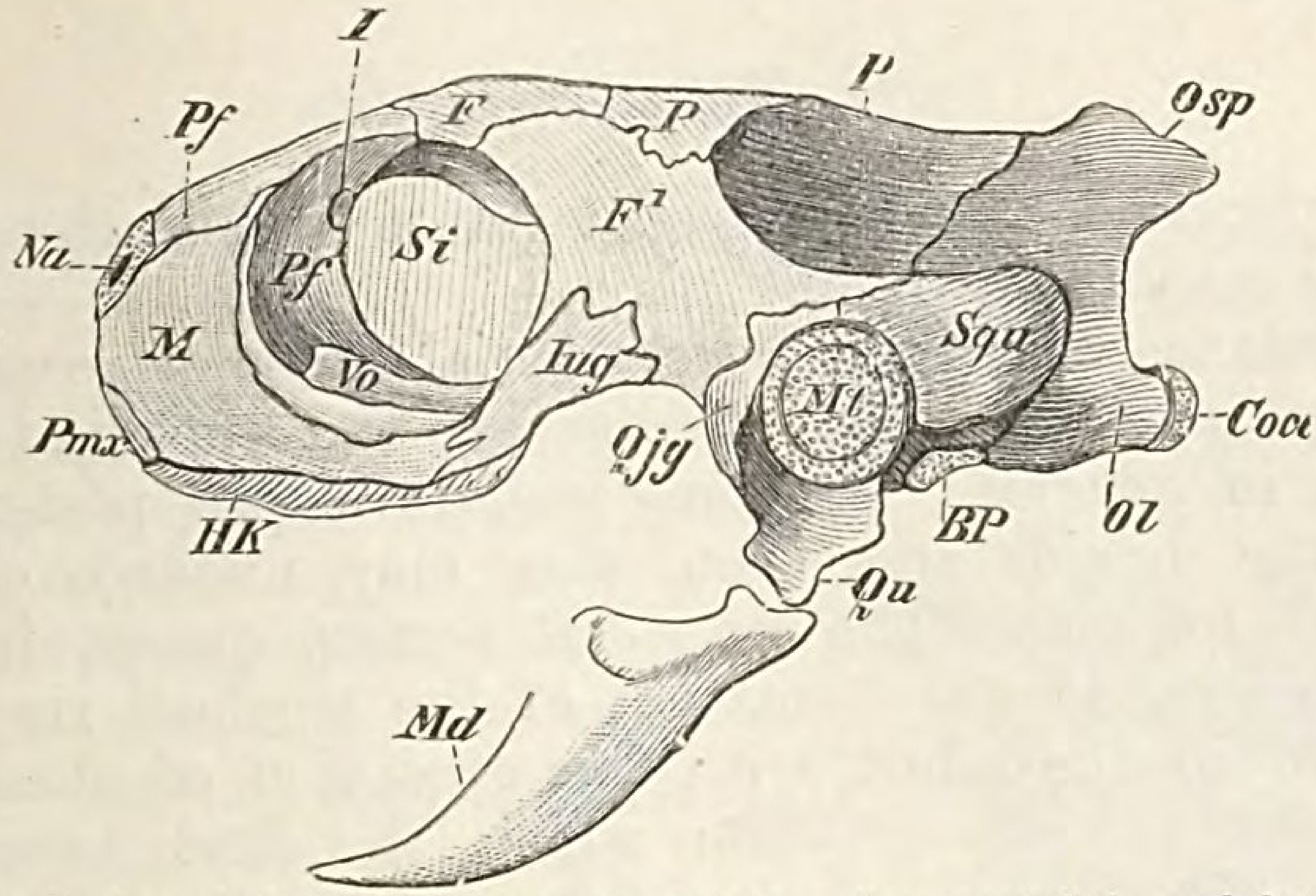


Fig. 935.—Lateral view of skull of **Emys europæa.** *Cocc.* occipital condyle; *F.* frontal; F_1. post-frontal; *I*, foramen by which the olfactory nerve enters the orbit; *Jug.* jugal; *M.* maxilla; *Md.* mandible; *Mt.* tympanic membrane; *Na.* external nares; *Ol*, ex-occipital; *Osp.* supra-occipital; *P.* parietal; *Pf.* pre-frontal; *P. mx.* pre-maxilla; *Qjg.* quadrato-jugal; *Qu.* quadrate; *Si.* inter-orbital septum; *Squ.* squamosal; *Vo.* vomer. (After Wiedersheim.)

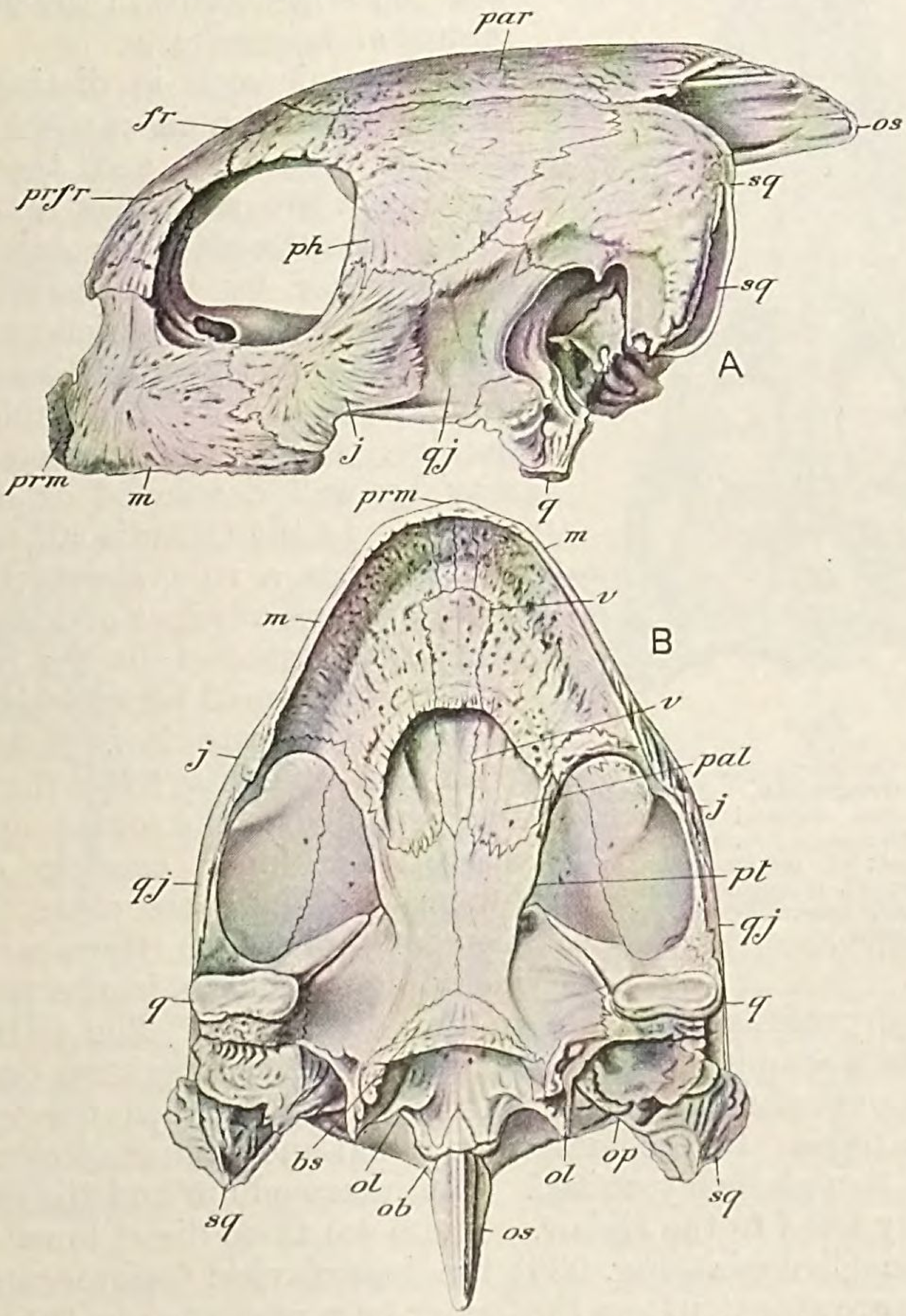


Fig. 936.—Ventral view of the skull of **Chelonia midas. bs.** basi-sphenoid; *j.* jugal; *m.* maxilla; **ob.** basi-occipital; **ol.** ex-occipital; **op.** opisthotic; **os.** supra-occipital; *pal.* palatine; *pt.* pterygoid; *prm.* pre-maxilla; **q.** quadrate; *qj.* quadrato-jugal; *sq.* squamosal; *v.* vomer. (After Hoffmann.)

a broad process of the pterygoid against which the inner surface of the mandibular ramus plays.

In accordance with their purely aërial mode of respiration, the *visceral arches* are much more reduced in the Reptilia than in the Amphibia in general. The only well-developed post-mandibular arch is the hyoid, and even this may undergo considerable reduction (Ophidia). The branchial arches, except in so far as they contribute to the formation of the tracheal rings, are not represented in the adult, with the exception of most Chelonia, in which the first branchial arch persists.

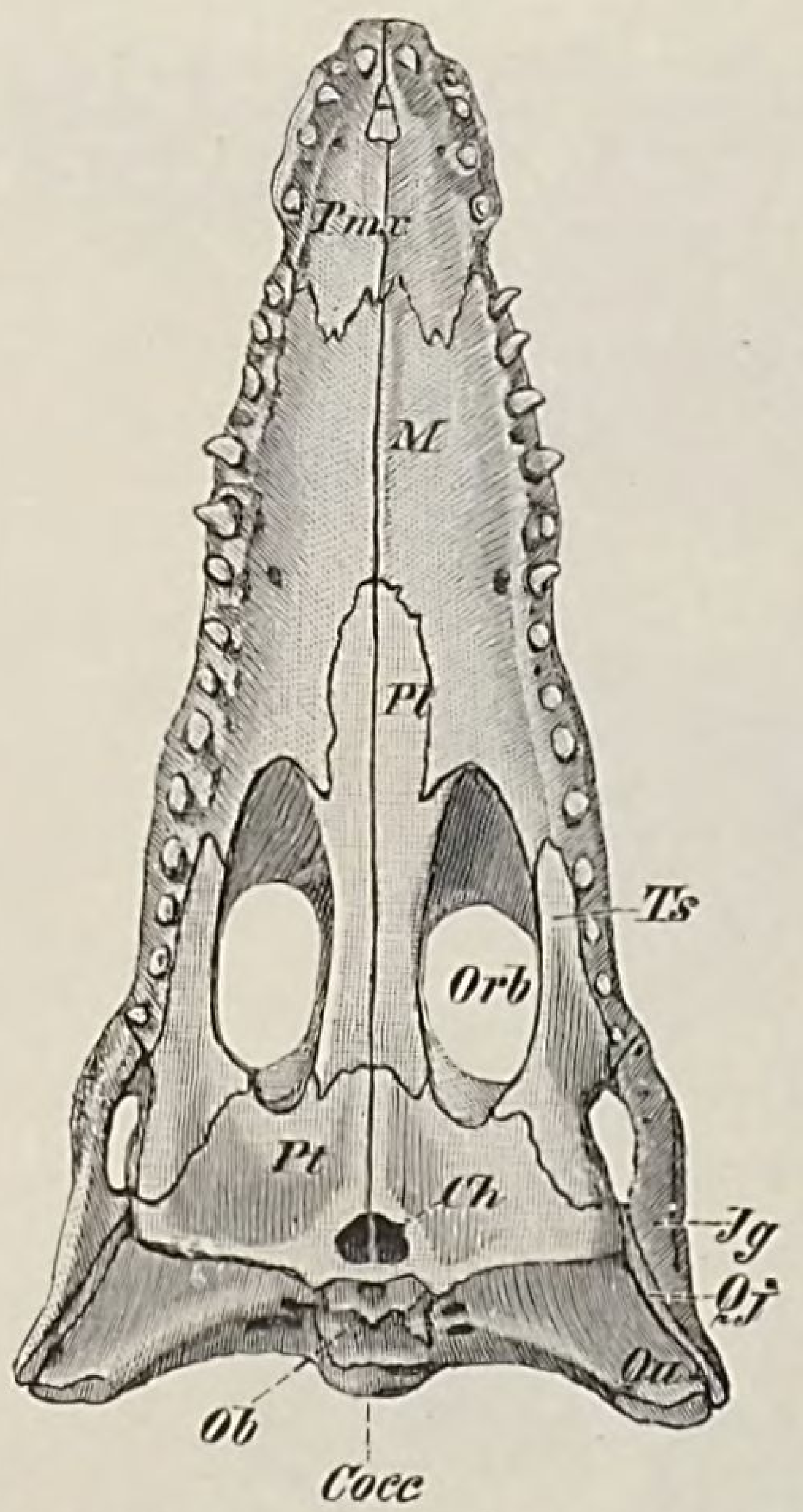


FIG. 937.—Ventral view of the skull of young **Crocodile.** *Ch*, posterior nares; *Cocc.* occipital condyle; *Jg.* jugal; *M.* maxilla; *Ob.* basi-occipital; *Orb.* orbit; *Pl.* palatine; *Pmx.* premaxillæ; *Pt.* pterygoid; *Qu.* quadrate; *Q.J.* quadrato-jugal. (From Wiedersheim.)

There is little variation in the structure of the limb-arches and skeleton of the limbs in the different groups of Lacertilia.

The pelvic arch is distinguished in the Lacertilia in general by its slender character; and the pubes and ischia are, as in fact is the case throughout the class, separated from one another by wide ischio-pubic foramina—a feature which markedly distinguishes the reptilian pelvis from that of the Amphibia. In limbless forms the pectoral arch may be well developed or may be absent. In the Ophidia all trace of limbs is, as a rule, absent; but in some Pythons vestiges of hind-limbs are to be detected in the form of two or three small bones which support a small horny claw.

In Hatteria (Fig. 928) there is a foramen above the outer and one above the inner condyle of the humerus. There are eleven carpal elements, of which there are four, including a pisiform, in the proximal row, two centrals, and five in the distal row. The pubes are united in a symphysis, in front of which is a cartilaginous epipubis. A large oval obturator foramen intervenes between the ischium and the pubis. In the tarsus the tibial and fibular elements are distinct, though firmly united. The intermedium and the centrale are firmly fixed to the tibiale. There are three distal tarsal bones.

In the Chelonia (Fig. 930) the interclavicle (episternum) and clavicles are absent, unless the former be represented by the median element of the plastron. The entire pectoral arch is a tri-radiate

structure of which the most ventral and posterior ray, ending in a free extremity, is the coracoid; while the other two are the pro-coracoid (or clavicle) and the scapula, with the supra-scapula, which are fused at their glenoid ends. The bones of the carpus have the typical arrangement, consisting of a proximal row of three, a distal row of five, and a centrale between the two. The pelvis resembles that of Lacertilia, except that it is broader and shorter. Both pubes and ischia meet in ventral symphyses. In the tarsus (Fig. 938) there is a single proximal bone, and four distalia.

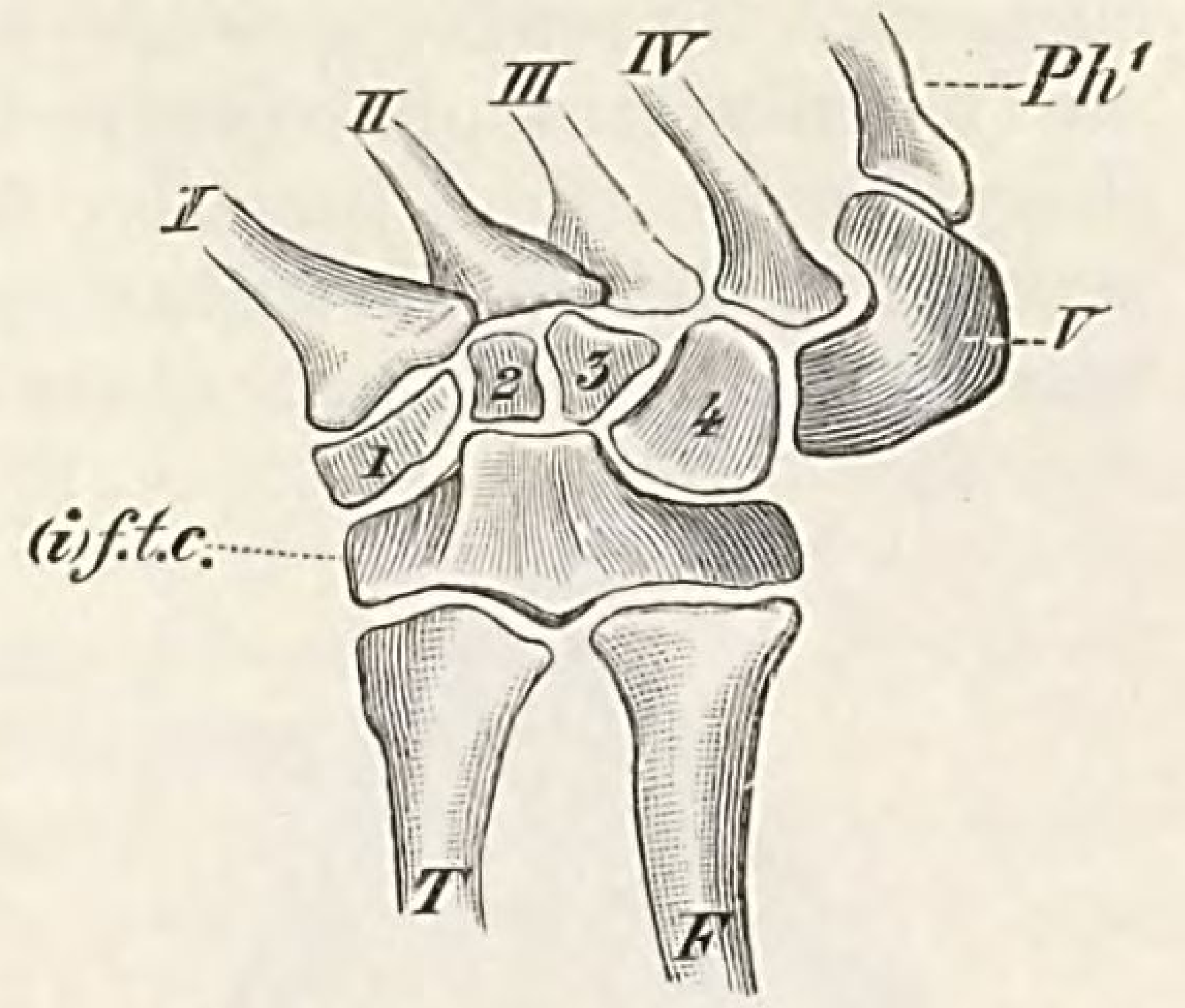


FIG. 938.—Tarsus of **Emys europæa** (right side) from above. *F.* fibula; *T.* tibia; *(i) f. t. c.* the united tarsals of the proximal row; *Ph'.* first phalanx of the fifth digit; 1—4. distal tarsals; *I—V*, metatarsals. (From Wiedersheim.)

In the Crocodilia also the clavicle is absent, but there is an episternum. There are two proximal carpal bones (Fig. 939), and two distal. There is *pisiform* (†) sometimes considered as a rudiment of a sixth digit. The pubes and ischia (Fig. 940) are fused; both meet in symphyses, the apposed ends being cartilaginous. The acetabular portion of the ilium is ossified as a distinct bone. In the tarsus (Fig. 941) there are two proximal bones—an *astragalo-scaphoid* and a *calcaneum*—the latter having a prominent calcaneal process; and two distal tarsal bones, together with a thin plate of cartilage supporting the first and second metatarsals. The missing fifth digit is represented by a rudimentary metatarsal.

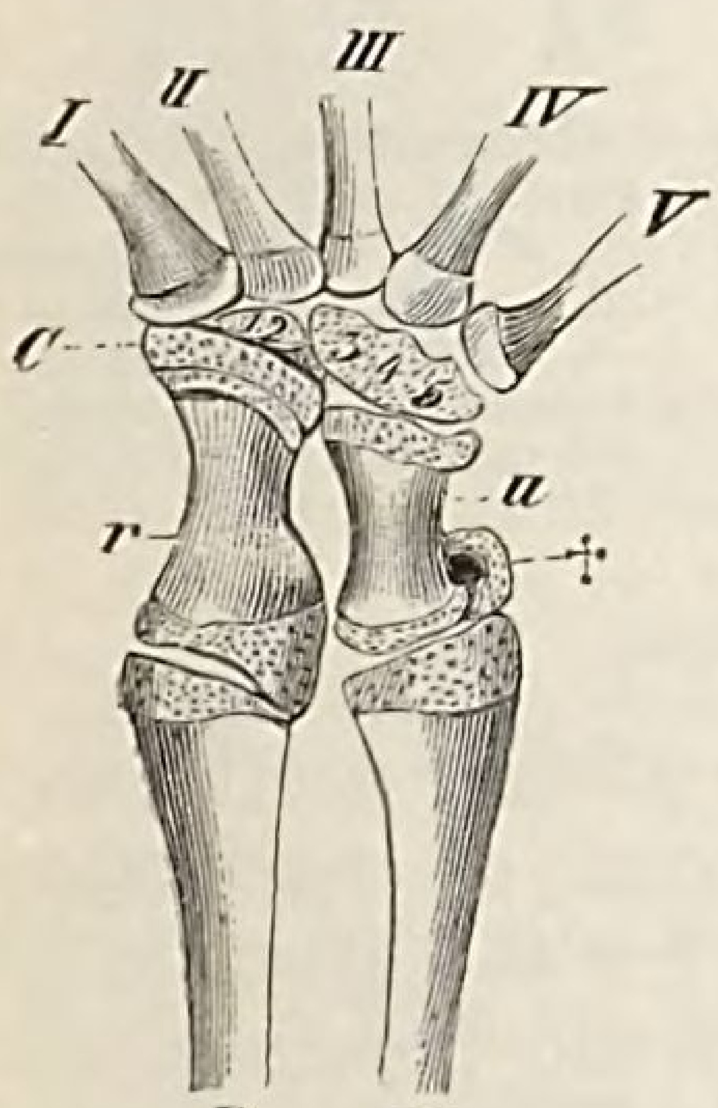


FIG. 939.—Carpus of young **Alligator.** *R.* radius; *U.* ulna; *C.* centrale; *r.* radiale; *u.* ulnare; 1—5, the five distal carpals (not yet ossified); 1 and 2 united into one, and also 3, 4 and 5; †, pisiform; *I—V*, the five metacarpals. (From Wiedersheim.)

Digestive Organs.—The form and arrangement of the teeth already described in the account of Lacerta prevail in the majority of Lizards. In some of them the palatine teeth are absent. The teeth are sometimes fixed by their bases to the summit of the ridge of the jaw (*acrodont* forms), sometimes fixed by their sides to the lateral surface of the ridge (*pleurodont*); they are never embedded in sockets in any recent form. A Mexican Lizard, *Heloderma*, differs from all the rest in having teeth which are grooved for the ducts of poison-glands. In the Snakes (Figs. 932, 933) teeth are

rarely developed on the pre-maxillæ, but are present on the maxillæ, palatines, pterygoids, and sometimes the transverse bones, as well as the dentary of the mandible. They may be of the same character throughout, solid elongated sharp-pointed teeth, which are usually strongly recurved, so that they have the character of sharp hooks, their function being rather to hold the prey and prevent it slipping from the mouth while being swallowed than to masticate it. Non-venomous Snakes possess only teeth of this character. In the venomous Snakes more or fewer of the maxillary teeth assume the character of poison-fangs. These are usually much larger

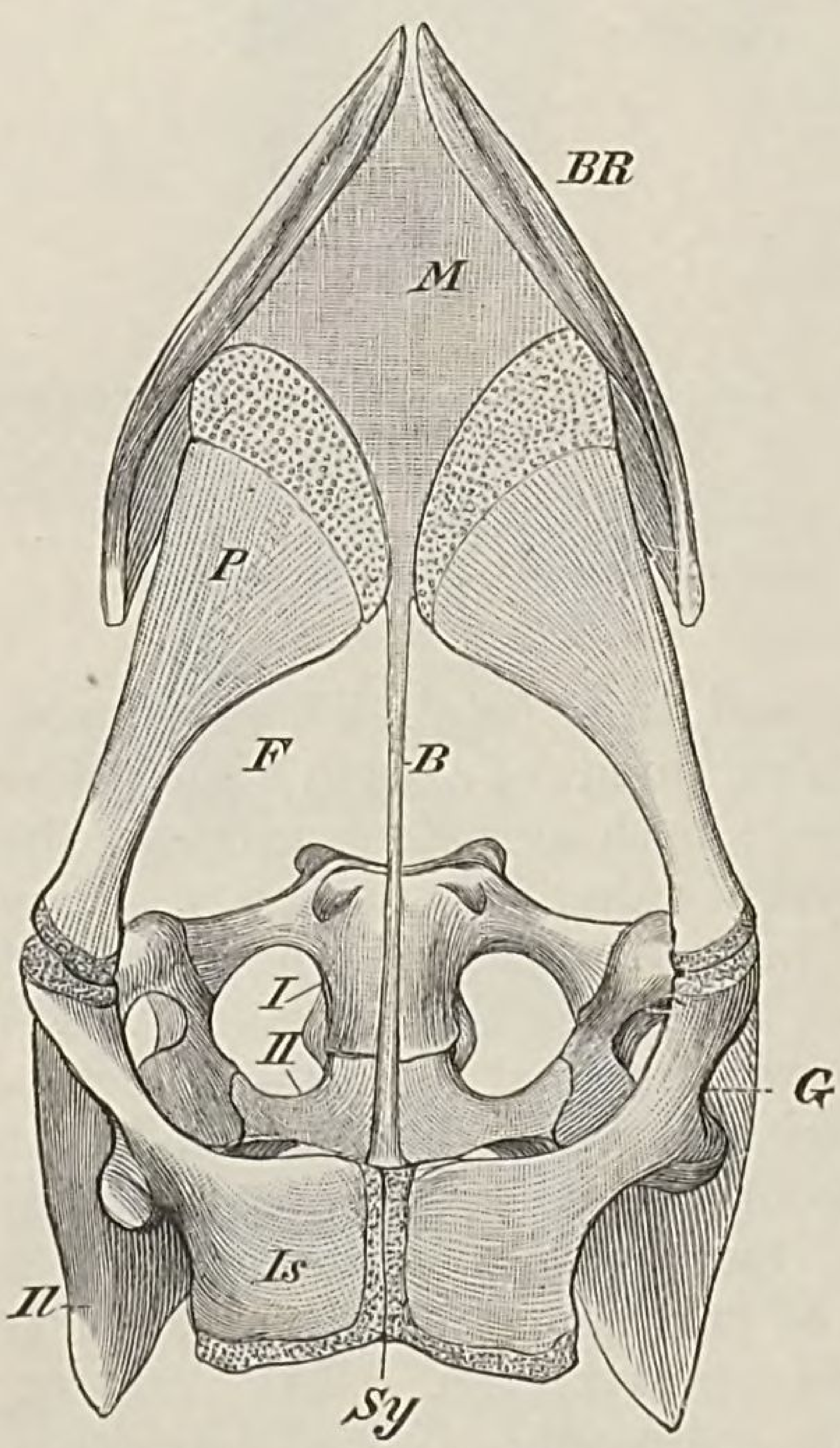


Fig. 940.—Pelvis of young **Alligator,** ventral aspect. *B*, fibrous band passing between the pubic and ischiadic symphyses; *BR.* last pair of abdominal ribs; *F.* obturator foramen; *G*, acetabulum; *Il* ilium; *Is.* ischium; *M.* fibrous membrane between the anterior ends of the two innominate bones and the last pair of abdominal ribs; *P.* pubis; *Sy.* ischiadic symphysis; *I*, *II*, first and second sacral vertebræ. (From Wiedersheim.)

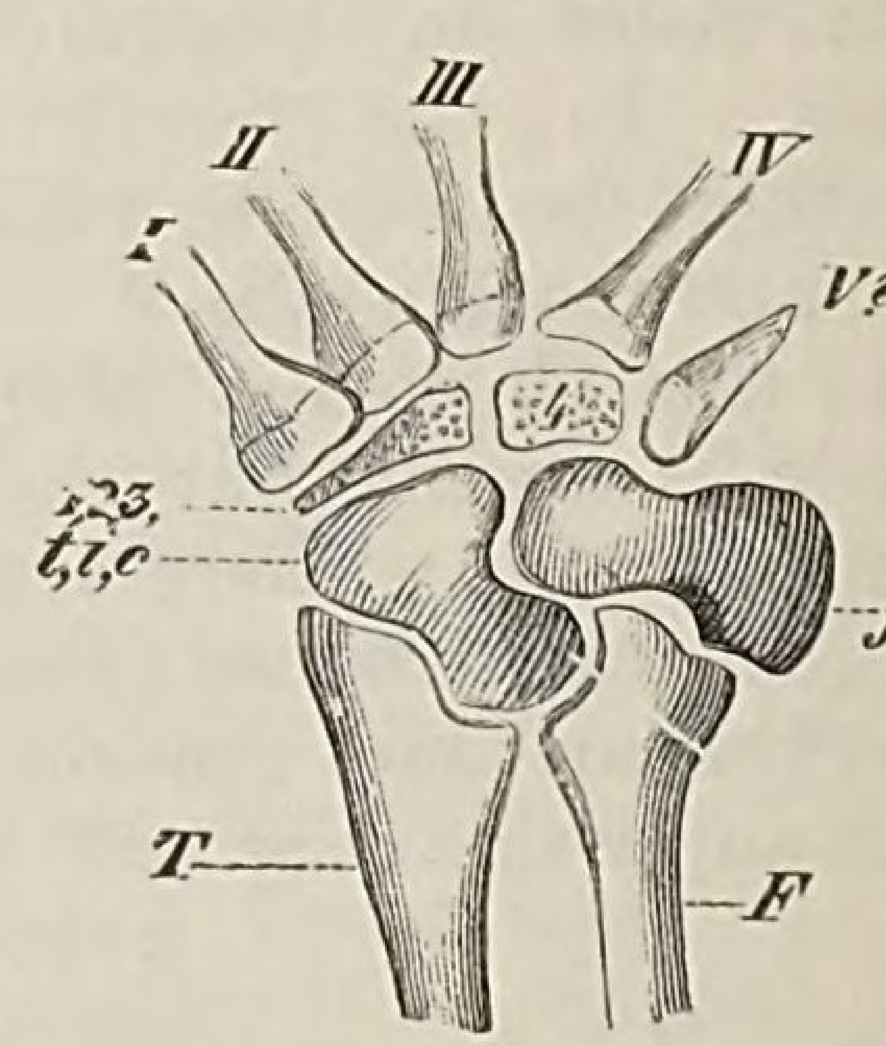


Fig. 941.—Tarsus of **Crocodile** (right side) from above. *F.* fibula; *T.* tibia; *t. i. c.* the astragalus formed of the united tibiale, intermedium and centrale; *f.* fibulare (calcaneum); 1—3, united first, second and third distal tarsals; 4, fourth tarsal; *I—IV*, first to fourth metatarsals; *V*?, fifth distal tarsal and fifth metatarsal. (From Wiedersheim.)

than the ordinary teeth, and either grooved or perforated by a canal for the passage of the duct of the poison-gland. In the Vipers (Fig. 933) there is a single large curved poison-fang with small reserve-fangs at its base, these being the only teeth borne by the maxilla, which is very short; in the venomous Colubrine Snakes the poison-fangs are either the most anterior or the most posterior of a considerable range of maxillary teeth. In the Vipers the large poison-fang is capable of being rotated through a considerable angle, and moved from a nearly horizontal position, in which it lies along the roof of the mouth embedded in folds of the mucous membrane, to a nearly vertical one, when

the Snake opens its mouth to strike its prey. The rotation of the maxilla is brought about by the backward or forward movement of the pterygoid with the palatine and transverse.

In Hatteria (Fig. 934) there are pointed, triangular, laterally-compressed teeth, arranged in two parallel rows, one along the maxilla, the other along the palatine. The teeth of the lower jaw, which are of similar character, bite in between these two upper rows, all the rows becoming worn down in the adult in such a way as to form continuous ridges. Each pre-maxilla bears a prominent, chisel-shaped incisor, represented in the young animal by two pointed teeth. In the young Hatteria a tooth has been found on each vomer—a condition exceptional among Reptiles.

In the Chelonia, teeth are entirely absent, the jaws being invested in a horny layer in such a way as to form a structure like a Bird's beak.

The Crocodilia have numerous teeth which are confined to the pre-maxillæ, the maxillæ, and the dentary. They are large, conical,

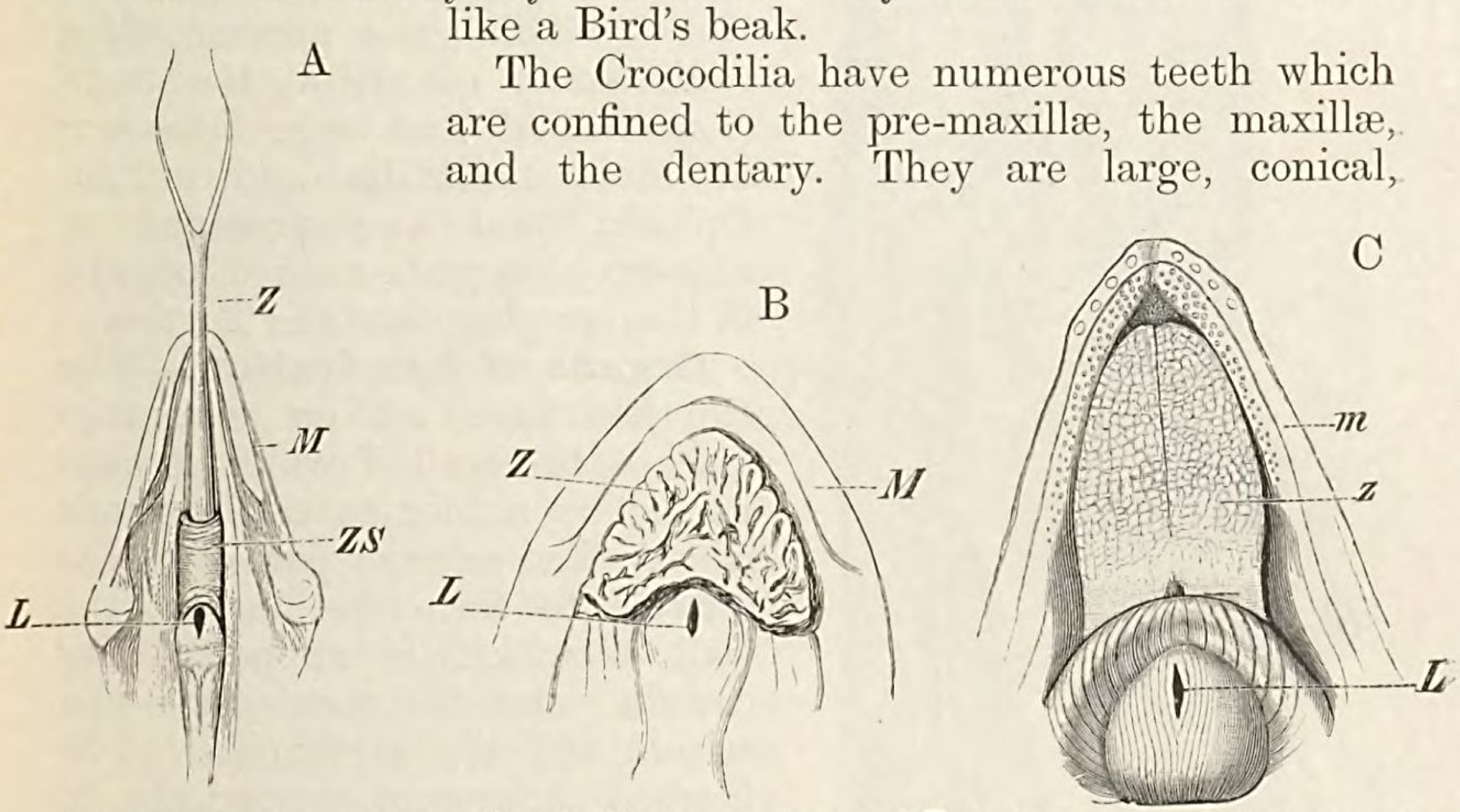


FIG. 942.—A, tongue of **Monitor indicus.** B, tongue of **Emys europæa.** C, tongue of **Alligator.** *L*, glottis; *M*. mandible; *Z*, tongue; *ZS*, tongue-sheath. (From Wiedersheim's *Comparative Anatomy*.)

hollow teeth devoid of roots, each lodged in its socket or alveolus, (*thecodont*) and each becoming replaced, when worn out, by a successor developed on its inner side.

A bifid tongue like that of Lacerta occurs in several families of Lacertilia. Others have a thick, short tongue, undivided in front and often provided with two long appendages behind. The Monitors (Fig. 942, A) have forked retractile tongues like those of Snakes. The tongue of the Chamæleons is an extremely remarkable organ; it is of sub-cylindrical form with an enlarged extremity, and is so extensile that it is capable of being darted out to a distance sometimes equalling or even exceeding the length of the trunk; this protrusion can be effected with lightning-like rapidity; and it is in this way that the animal catches the Insects which

constitute its food. The tongue in Snakes is slender and bifid, capable of being retracted into a basal sheath, and is highly sensitive, being used chiefly as a tactile organ. The tongue of the Crocodilia (C) is a thick immobile mass extending between the rami of the mandible. In some of the Chelonia (B) the tongue is immobile; in others it is protrusible, sometimes bifid.

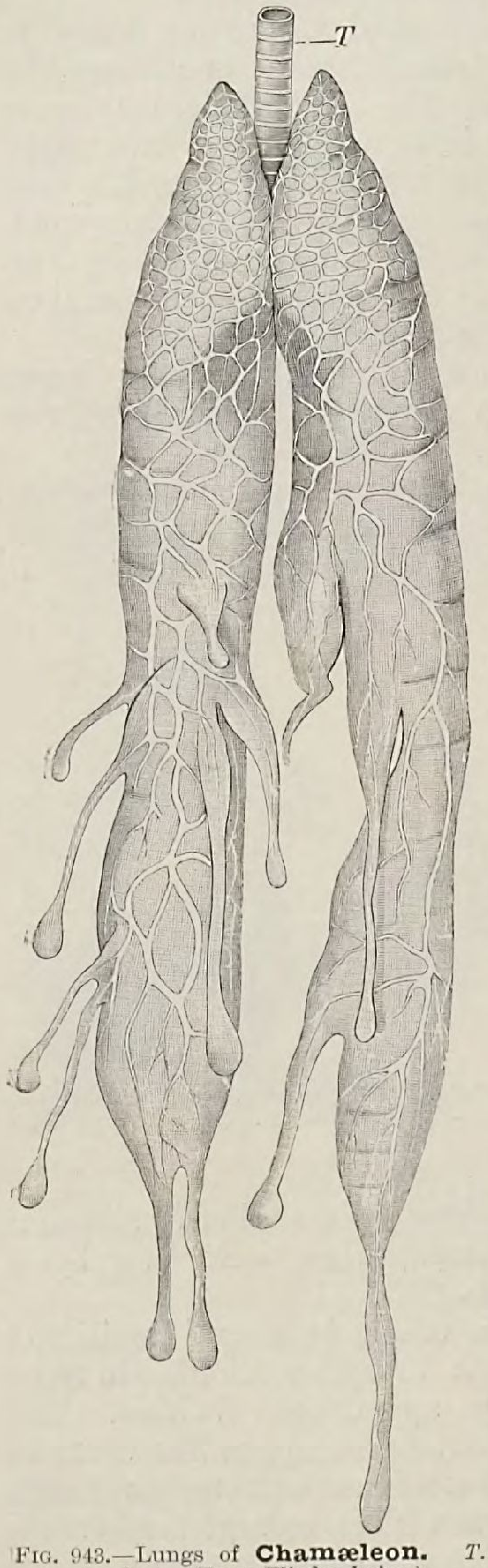


FIG. 943.—Lungs of **Chamæleon.** *T.* trachea. (From Wiedersheim.)

In the enteric canal of the Reptiles the principal special features to be noticed are the muscular gizzard-like stomach of the Crocodilia, the presence of a rudimentary cœcum at the junction of small and large intestines in most Lacertilia and in the Ophidia, and the presence of numerous large cornified papillæ in the œsophagus of the Turtles.

Organs of Respiration.—The Reptiles have all an elongated trachea, the wall of which is supported by numerous cartilaginous rings. The anterior part of this is dilated to form the *larynx*, the wall of which is supported by certain special cartilages — the cricoid and the arytenoids. The trachea bifurcates posteriorly to form two bronchi, right and left, one passing to each lung. In some of the Chelonia its lumen is divided internally by a vertical septum. The lungs of the Lacertilia and Ophidia are of the simple sac-like character already described in the case of the Lizard. In some the lung is incompletely divided internally into two portions—an anterior respiratory part with sacculated walls, and a posterior part with smooth, not highly vascular walls, having mainly the function of a reservoir. The only additional complication to be specially noted is the presence in the Chamæleons (Fig. 943) of a

number of diverticula or *air-sacs* which are capable of being inflated, causing an increase in the bulk of the animal which doubtless has an effect on assailants. In the snake-like Lizards the right lung is larger than the left, and in the Amphisbænians the latter is entirely aborted. In the Snakes a similar reduction or abortion of the left lung is observable. In the Crocodilia and Chelonia the lungs are of a more complex character, being divided internally by septa into a number of chambers.

Organs of Circulation.—In the heart (Fig. 944) the sinus venosus is always distinct, and is divided into two parts by a septum; its aperture of communication with the right auricle is guarded by valves. There are, as in the Amphibia, always two quite distinct auricles, the right receiving the venous blood from the body, the left the oxygenated blood brought from the lungs by the pulmonary veins. But a vital point of difference between the heart of the Reptile and that of the Amphibian is that in the former the ventricle is always more or less completely divided into right and left portions. In all the Lacertilia, Ophidia and Chelonia (Fig. 945) the structure is essentially what has been described in Lacerta, the ventricular septum being well-developed, but not completely closing off the left-hand portion of the cavity of the ventricle from the right (*cavum pulmonale*). The left-hand portion, which is much the larger, is further imperfectly divided into two parts—the *cavum arteriosum* on the left and the *cavum venosum* on the right—by the two elongated flaps of the auriculo-ventricular valve, which project freely into the cavity of the ventricle. From the cavum pulmonale arises the pulmonary artery, and from the cavum venosum, the two aortic arches. When the auricles contract the cavum venosum becomes filled with venous blood from the right auricle, and the cavum arteriosum with arterial blood from the left auricle; the cavum pulmonale becomes filled with venous blood which flows into it past the edges of the incomplete septum. When

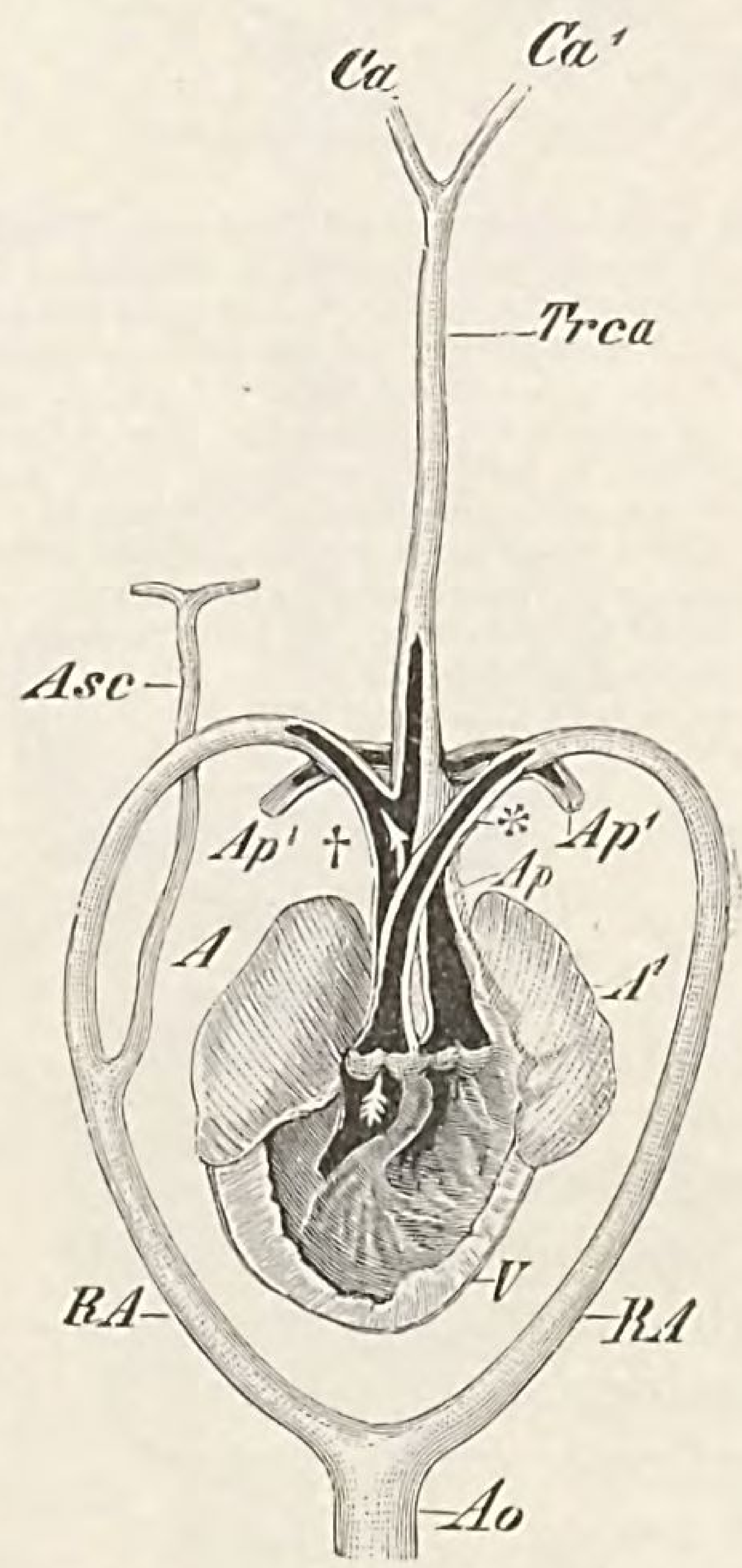


FIG. 944.—Heart of **Monitor** (*Varanus*) dissected to show the cavity of the ventricle and the vessels leading out from it. *A. A'.* auricles; *Ao*, dorsal aorta; *Ap*, *Ap'*, pulmonary arteries; *Asc.* subclavian artery; *Ca. Ca'.* carotids; *RA*, *RA*, roots of dorsal aorta; *Trca*, innominate trunk; *V.* ventricle; †, right aortic arch; *, left aortic arch. (From Wiedersheim.)

the ventricle contracts, its walls come in contact with the edges of the septum, and the cavum pulmonale becomes cut off from the rest of the ventricle. The further contraction consequently results in the venous blood of the cavum pulmonale being driven out through the pulmonary artery to the lungs, while the blood that remains in the remainder of the ventricle (arterial and mixed) is compelled to pass out through the aorta. But in the Crocodilia (Fig. 946) the cavity is completely divided, so that there we may speak of distinct right and left ventricles. From the right arises the pulmonary artery and the left aortic arch; from the left the right aortic arch only. The right and left arches cross one another and where their walls are in contact is an aperture—the *foramen Panizzæ*—placing their cavities in communication.

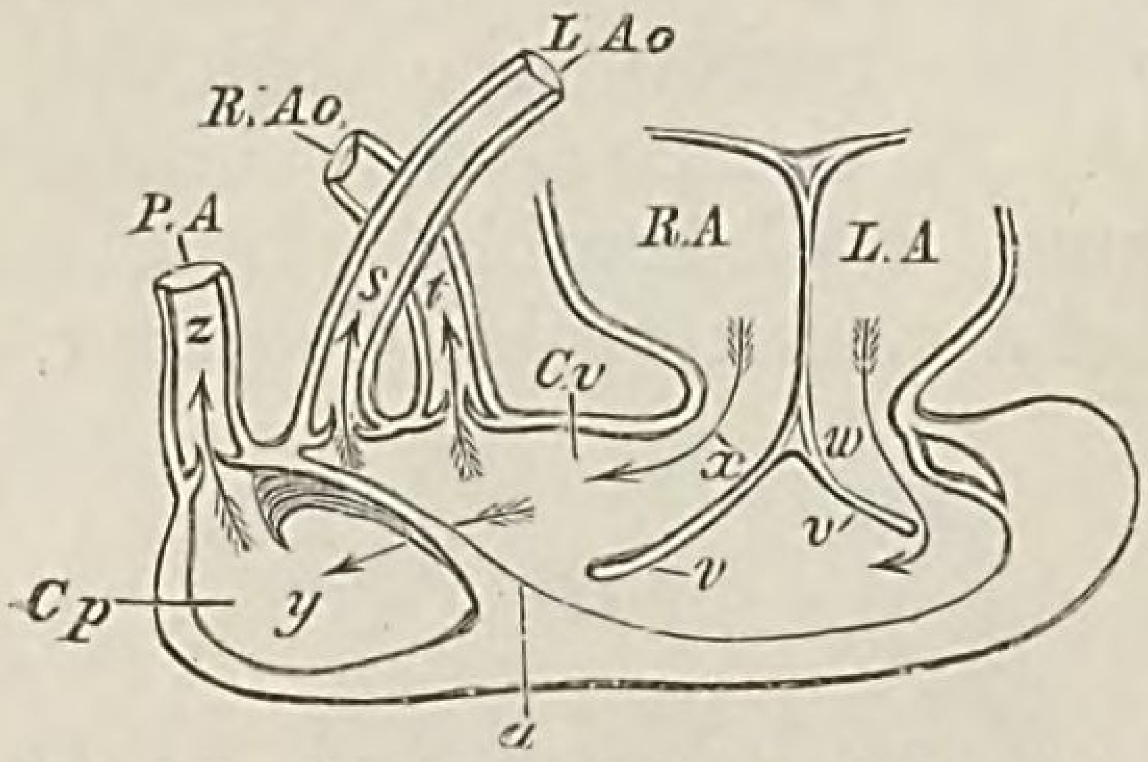


FIG. 945.—Diagram of heart of **Turtle.** *a*, incomplete ventricular septum; *C. p.* cavum pulmonale; *C. v.* cavum venosum; *L. A.* left auricle; *L. ao.* left aortic arch; *P. A.* pulmonary artery; *R. A.* right auricle; *s*, arrow showing the course of blood in left aorta; *t*, in right aorta; *v. v'.* auriculo-ventricular valves; *w*, arrow showing the course of blood in left auriculo-ventricular aperture; *x*, in right; *y*, between cavum venosum and cavum pulmonale; *z*, in pulmonary artery. (After Huxley.)

The **brain** of Reptiles is somewhat more highly organised than that of the Amphibia. The brain substance exhibits a distinction into superficial grey layer or cortex, containing pyramidal nerve cells, and central white medulla, not observable in lower groups. The cerebral hemispheres are well developed in all. The mid-brain consists usually of two closely-approximated oval optic lobes; rarely it is divided superficially into four. The cerebellum is always of small size, except in the Crocodilia (Fig. 947), in which it is comparatively highly developed, and consists of a median and two lateral lobes.

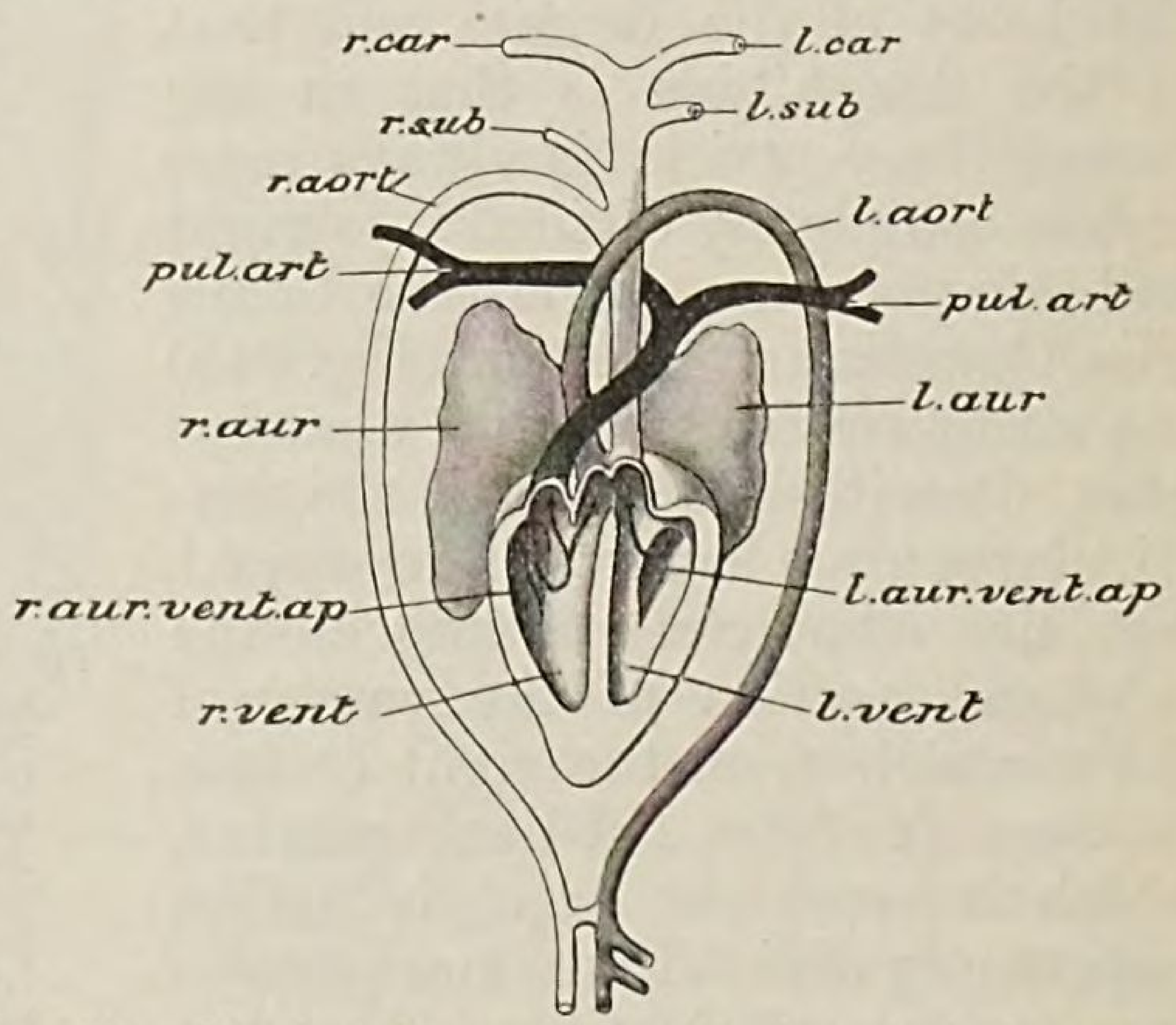


FIG. 946.—Heart of **Crocodile** with the principal arteries (diagrammatic). The arrows show the direction of the arterial and venous currents. *l. aort.* left aortic arch; *l. aur.* left auricle; *l. aur. vent. ap.* left auriculo-ventricular aperture; *l. car.* left carotid; *l. sub.* left subclavian; *l. vent.* left ventricle; *pul. art.* pulmonary artery; *r. aort.* right aortic arch; *r. aur.* right auricle; *r. aur. vent. ap.* right auriculo-ventricular aperture; *r. car.* right carotid; *r. sub.* right subclavian; *r. vent.* right ventricle. (From Hertwig's *Lehrbuch.*)

Sensory Organs.—In most Lacertilia, but not in the Ophidia, the nasal cavity consists of two parts—an outer or vestibule and an inner or olfactory chamber—the latter having the sense-cells in its walls, and containing a turbinal bone. In the Turtles each nasal chamber is divided into two passages, an upper and a lower, and the same holds good of the hinder part of the elongated nasal chamber of the Crocodilia.

Jacobson's organs (Fig. 917) are present in Lizards and Snakes, absent in Chelonia and Crocodilia in the adult condition.

The eyes are relatively large, with a cartilaginous sclerotic in which a ring of bony plates (Fig. 918) is developed in some cases. The muscular fibres of the iris are striated. A pecten is present in most. Most Reptiles have both upper and lower eyelids and nictitating membrane. The greater number of the Geckos and all the Snakes constitute exceptions, movable eyelids being absent in both these groups; in the former the integument passes uninterruptedly over the cornea with a transparent spot for the admission of the light; in the Snakes there is a similar modification, but the study of the development shows that the transparent area is derived from the nictitating membrane which becomes drawn over the cornea and permanently fixed. In the Chamæleons there is a single circular eyelid with a central aperture.

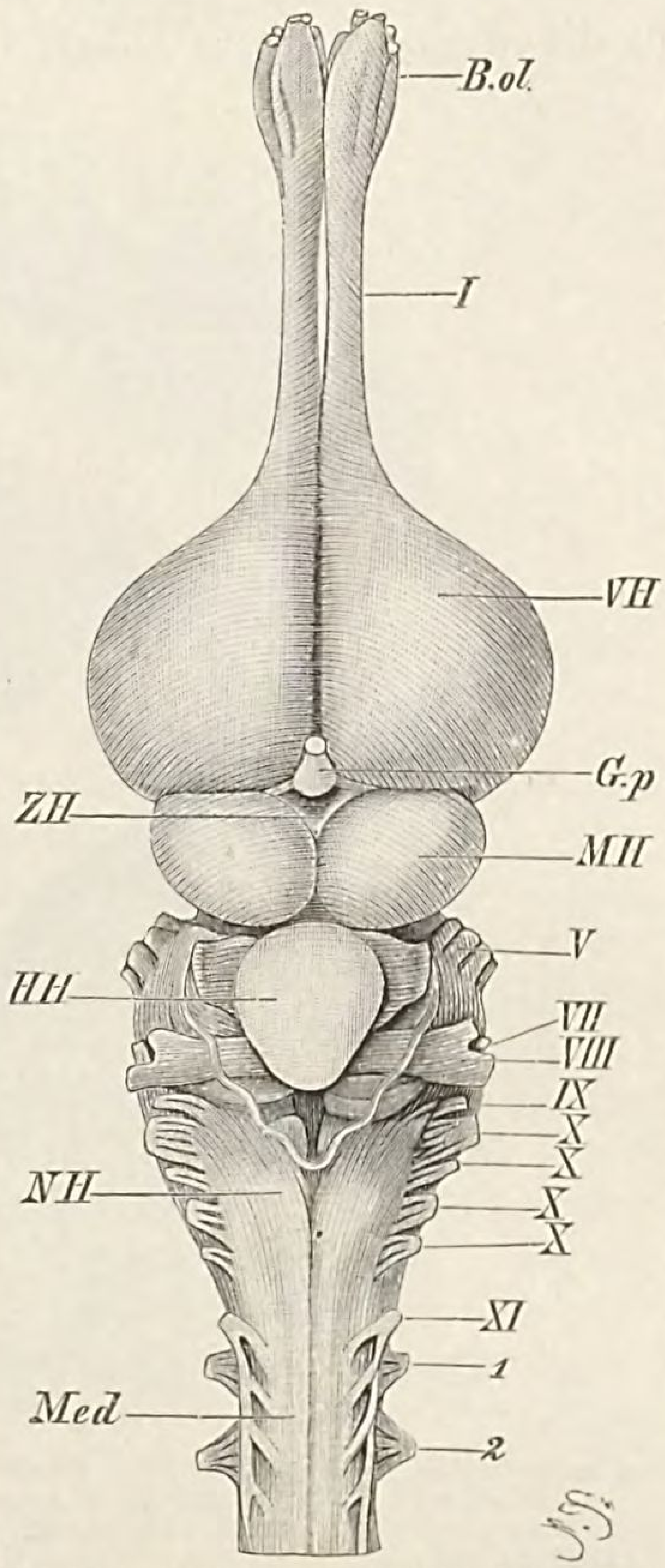


FIG. 947.—Brain of **Alligator,** from above *B. ol.* olfactory bulb; *G, p,* epiphysis; *HH,* cerebellum; *Med,* spinal cord; *M, H,* optic lobes; *NH,* medulla oblongata; *VH,* cerebral hemispheres; *I—XI,* cranial nerves; 1, 2, first and second spinal nerves. (From Wiedersheim.)

The middle ear is absent in the Snakes, though a columella auris is present, embedded in muscular and fibrous tissue.

Developed in close relation to the epiphysis there is in many Lizards (*Lacerta*, *Varanus*, *Anguis*, *Grammatophora* and others) and in Hatteria, a remarkable eye-like organ—the *pineal eye* (Fig. 948), which is situated in the parietal foramen of the cranial roof

immediately under the integument, and covered over by a specially modified, transparent scale. Like the epiphysis itself, the pineal eye is developed as a hollow outgrowth of the roof of the diencephalon; the distal end of this becomes constricted off as a hollow sphere while the remainder becomes converted into a nerve. The wall of the hollow sphere becomes divergently modified on opposite sides; the distal side becomes modified to

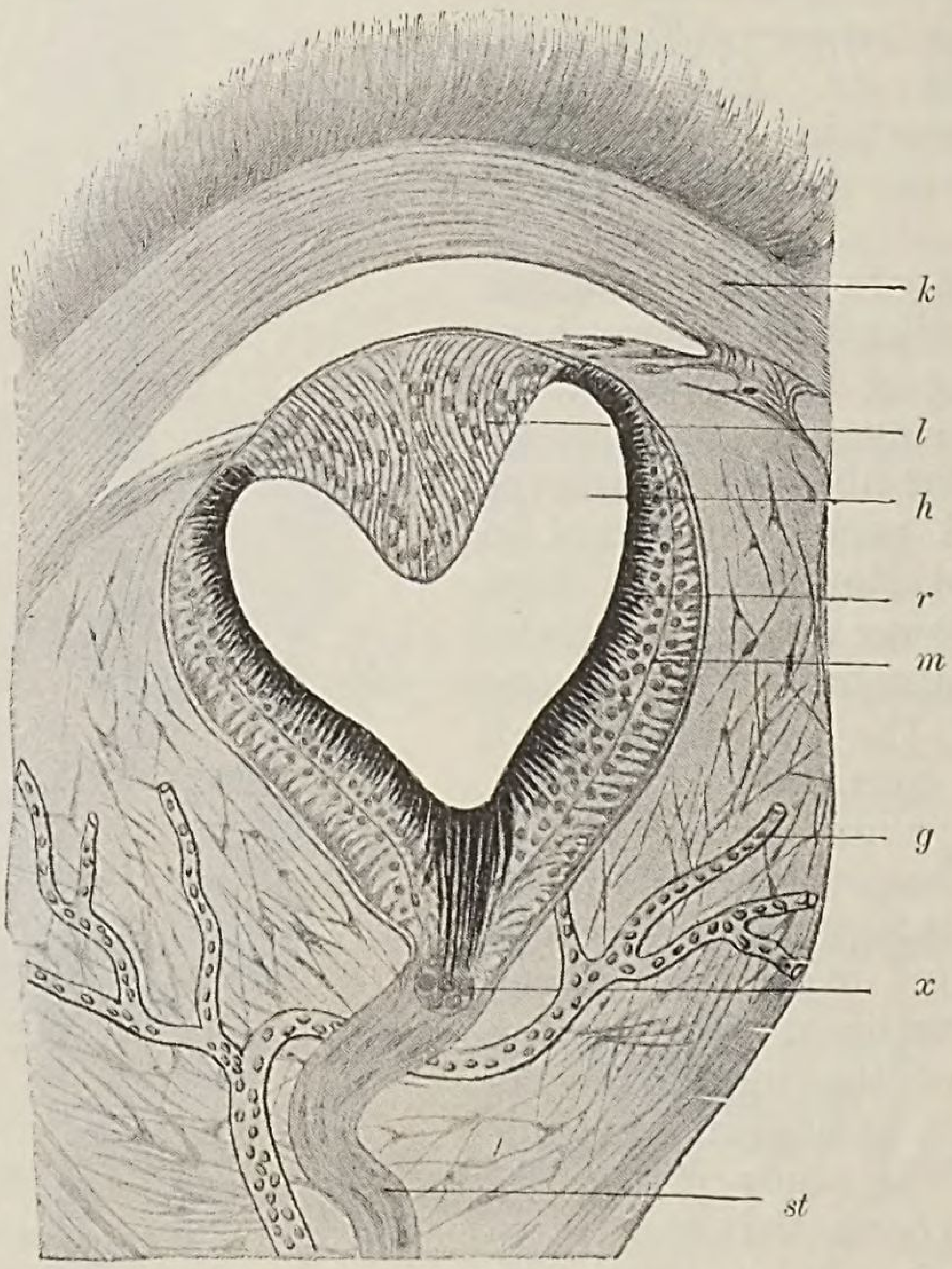


FIG. 948.—Section of the pineal eye of **Hatteria punctata.** *g*, blood-vessels; *h*, cavity of the eye filled with fluid; *k*, capsule of connective tissue; *l*. lens; *m*. molecular layer of the retina; *r*. retina; *st*. stalk of the pineal eye; *x*, cells in the stalk. (From Wiedersheim, after Baldwin Spencer.)

form a lens-like thickening (*l*), the proximal forms a membrane several layers in thickness—the *retina* (*r*.)—the whole is enclosed in a capsule of connective tissue (*k*.). The nerve degenerates before the animal reaches maturity, so that the organ would appear—though evidently, from its structure, an organ of sight—to have now entirely or nearly lost its function.

Reproductive Organs.—The description already given of the reproductive organs of the Lizard (p. 310) applies, so far as all the leading features are concerned, to all the Lacertilia and to the Ophidia; in Hatteria the copulatory sacs are absent. In the

Crocodilia and Chelonia, instead of the copulatory sacs there is a median solid penis attached to the wall of the cloaca, and a small process or *clitoris* occurs in a corresponding position in the female. Though fertilisation is always internal, most Reptilia are oviparous, laying eggs enclosed in a tough, parchment-like or calcified shell. These are usually deposited in holes and left to hatch by the heat of the sun. In the Crocodiles they are deposited in a rough nest and guarded by the mother. In all cases development has only progressed to a very early stage when the deposition of the eggs takes place, and it is only after a more or less prolonged period of incubation that the young, fully formed in every respect, emerge from the shell and shift for themselves.

Many Lizards, however, and also many Snakes are viviparous, the ova being developed in the interior of the oviduct, and the young reaching the exterior in the completely formed condition.

Development.—In all the Reptilia the segmentation is meroblastic, being confined to a germinal disc of protoplasm situated on one side of the yolk. This divides to form a patch of cells which gradually extend as a two-layered sheet, the blastoderm, over the surface of the ovum. As the blastoderm extends (Fig. 949) it becomes distinguishable into a central clearer area—*area pellucida* (*a. pel.*)—and a peripheral whitish zone—*area opaca* (*a. op.*). On the former now appears an elliptical thickened patch —the *embryonic shield* (*emb. s.*)—which is formed by the ectoderm cells in this region assuming a cylindrical form while remaining flat elsewhere. On the embryonic shield, in a direction corresponding to the long axis of the future embryo, appears a thickening due to a proliferation of the ectoderm cells, and here the upper and lower layers coalesce (*primitive streak*); this is the preliminary to the formation of the blastopore and neurenteric canal. In front of this the lower layer develops a thickening which is the rudiment of the notochord and the central portion of the mesoderm. A depression appears on the surface of the ectodermal thickening and this grows inwards, giving rise to an invagination—the blastopore (*blp.*). The formation of the archenteric cavity and of the definite *enteric endoderm* layer is, in Reptiles with a more primitive mode of development, subsequent to, and dependent on, this process of invagination; in others, the process of invagination is delayed, and takes place only after the endoderm and the beginnings of the enteric cavity have become established. In either case the invagination communicates with the primitive enteron, forming a neurenteric passage which persists for some time.

In front of the blastopore a longitudinal depression bounded by a pair of longitudinal folds (*med. f.*) is the beginning of the medullary groove. As this becomes closed, it encloses in its posterior portion the blastopore or dorsal opening of the neurenteric canal. At the sides of the medullary groove appear the protovertebræ

(*prot. v.*), and below it a cord of endoderm cells, the rudiment of the notochord; the general history of these parts has already been sketched in the section on the Craniata, and further details will be given in the account of the development of Birds, which agrees

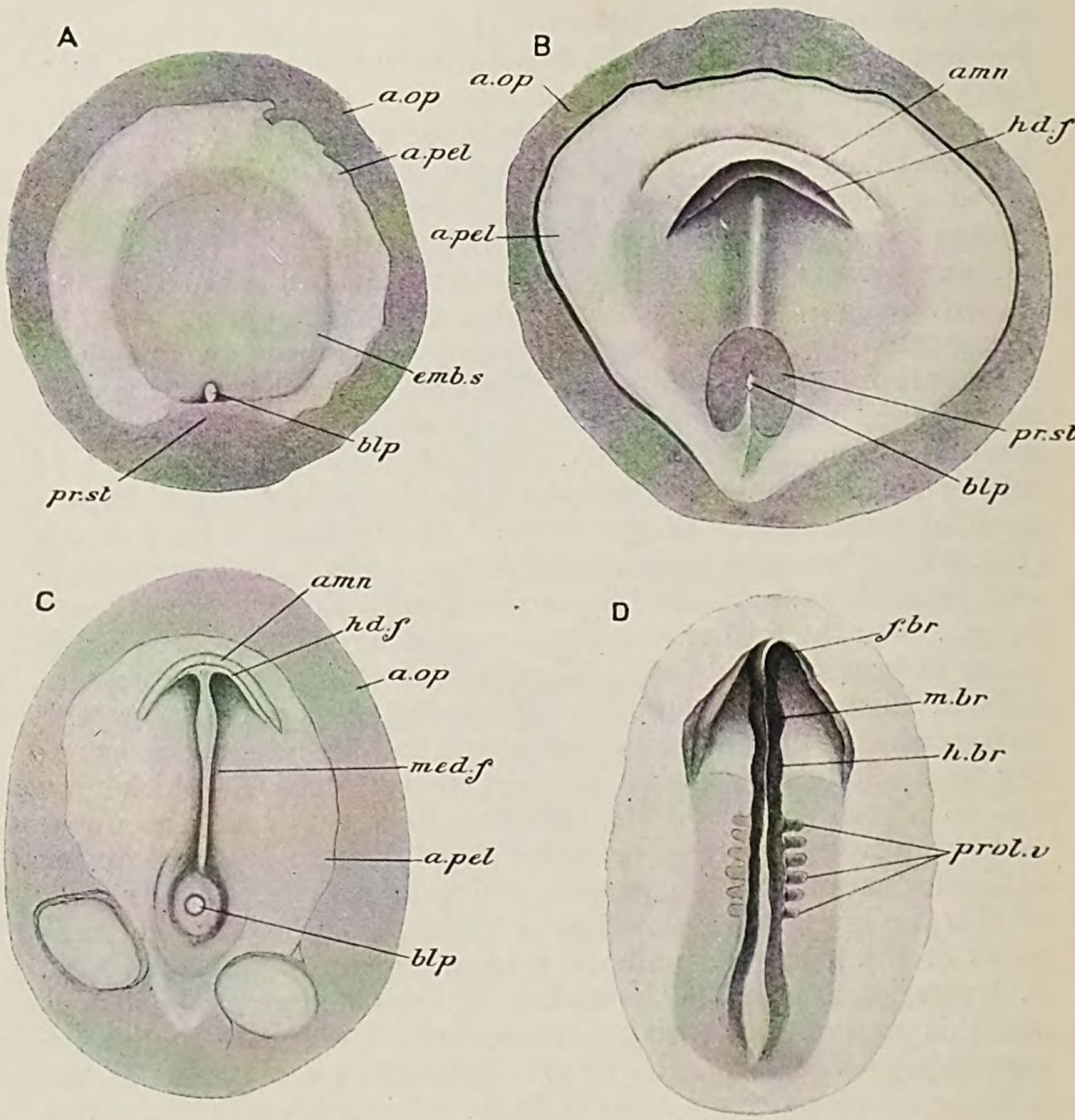


FIG. 949.—A—D, early stages in the development of the **Alligator.** *A*, early stage with embryonic shield, primitive streak and blastopore; *B*, considerably later stage in which the medullary groove has become formed, together with the head-fold of the embryo and the head-fold of the amnion; *C*, somewhat later stage with well-developed medullary folds and medullary groove; *D*, later stage in which the medullary groove has become partly closed in by the medullary folds and in which six pairs of protovertebræ have become developed. *amn.* amnion; *a. op.* area opaca; *a. pel.* area pellucida; *blp.* blastopore; *emb. s.* embryonic shield; *f. br.* fore-brain; *h. br.* hind-brain; *hd. f.* head-fold; *m. br.* mid-brain; *med. f.* medullary folds; *prot. v.* protovertebræ. (After S. F. Clarke.)

with that of Reptiles in all essential respects. Under the head of Birds also will be found an account of the formation of the characteristic fœtal membranes, the amnion and the allantois, which applies in all essential respects to the Reptilia as well.

Ethology.—The Lizards are, for the most part, terrestrial animals, usually extremely active in their movements and endowed with keen senses. The majority readily ascend trees, and many kinds are habitually arboreal; but the Chamæleons are the only members of the group which have special modifications of their structure in adaptation with an arboreal mode of life. The Skinks and the Amphisbænians are swift and skilful burrowers. The Geckos are enabled by the aid of the sucker-like discs on the ends of their toes to run readily over vertical or overhanging smooth surfaces. A few, on the other hand (Water-Lizards), live habitually in fresh water. The Flying Lizards (*Draco*) are arboreal, and make use of their wings—or, to speak more accurately, aëroplane or parachute—to enable them to take short flights from branch to branch. Chlamydosaurus is exceptional in frequently running on the hind-feet, with the fore-feet entirely elevated from the ground. A tolerably high temperature is essential for the maintenance of the vital activities of Lizards, low temperatures bringing on an inert condition, which usually passes during the coldest part of the year into a state of suspended animation or hibernation. The food of Lizards is entirely of an animal nature. The smaller kinds prey on Insects of all kinds, and on Worms. Chamæleons, also, feed on Insects, which they capture by darting out the extensile tongue covered with a viscid secretion. Other Lizards supplement their insect diet, when opportunity offers, with small Reptiles of various kinds, Frogs and Newts, small Birds and their eggs, and small Mammals, such as Mice and the like. The larger kinds, such as the Monitors and Iguanas, prey exclusively on other vertebrates; some, on occasion, are carrion-feeders. Most Lizards lay eggs enclosed in a tough calcified shell. These they simply bury in the earth, leaving them to be hatched by the heat of sun. Some, however, are viviparous; in all cases the young are left to shift for themselves as soon as they are born.

Most of the Snakes are also extremely active and alert in their movements; and most are very intolerant of cold, undergoing a hibernation of greater or less duration during the winter season. Many live habitually on the surface of the ground—some kinds by preference in sandy places or among rocks, others among long herbage. Some (Tree-Snakes) live habitually among the branches of trees. Others (Fresh-water Snakes) inhabit fresh water; others (Sea-Snakes) live in the sea. The mode of locomotion of Snakes on the ground is extremely characteristic, the reptile moving along by a series of horizontal undulations brought about by contractions of the muscles inserted into the ribs, any inequalities on the surface of the ground serving as fulcra against which the free posterior edges of the ventral shields (which are firmly connected with the ends of the ribs) are enabled to act. The burrowing Blind-Snakes and other families of small Snakes feed on Insects

and Worms. All the rest prey on vertebrates of various kinds, Fishes, Frogs, Lizards, Snakes, Birds and their eggs, and Mammals. The Pythons and Boas kill their prey by constriction, winding their body closely round it and drawing the coils tight till the victim is crushed or asphyxiated. Some other non-venomous Snakes kill with bites of their numerous sharp teeth. The venomous Snakes sometimes, when the prey is a small and weak animal such as a Frog, swallow it alive: usually they kill it with the venom of their poison-fangs.

When a venomous Snake strikes, the poison is pressed out from the poison-gland by the contraction of the masseter (Fig. 950, *Mc*), one of the muscles which raise the lower jaw; it is thus forced along the duct (*Gc*) to the aperture (*za*), and injected into the wound made by the fang. The effect is to produce acute pain with increasing lethargy and weakness, and in the

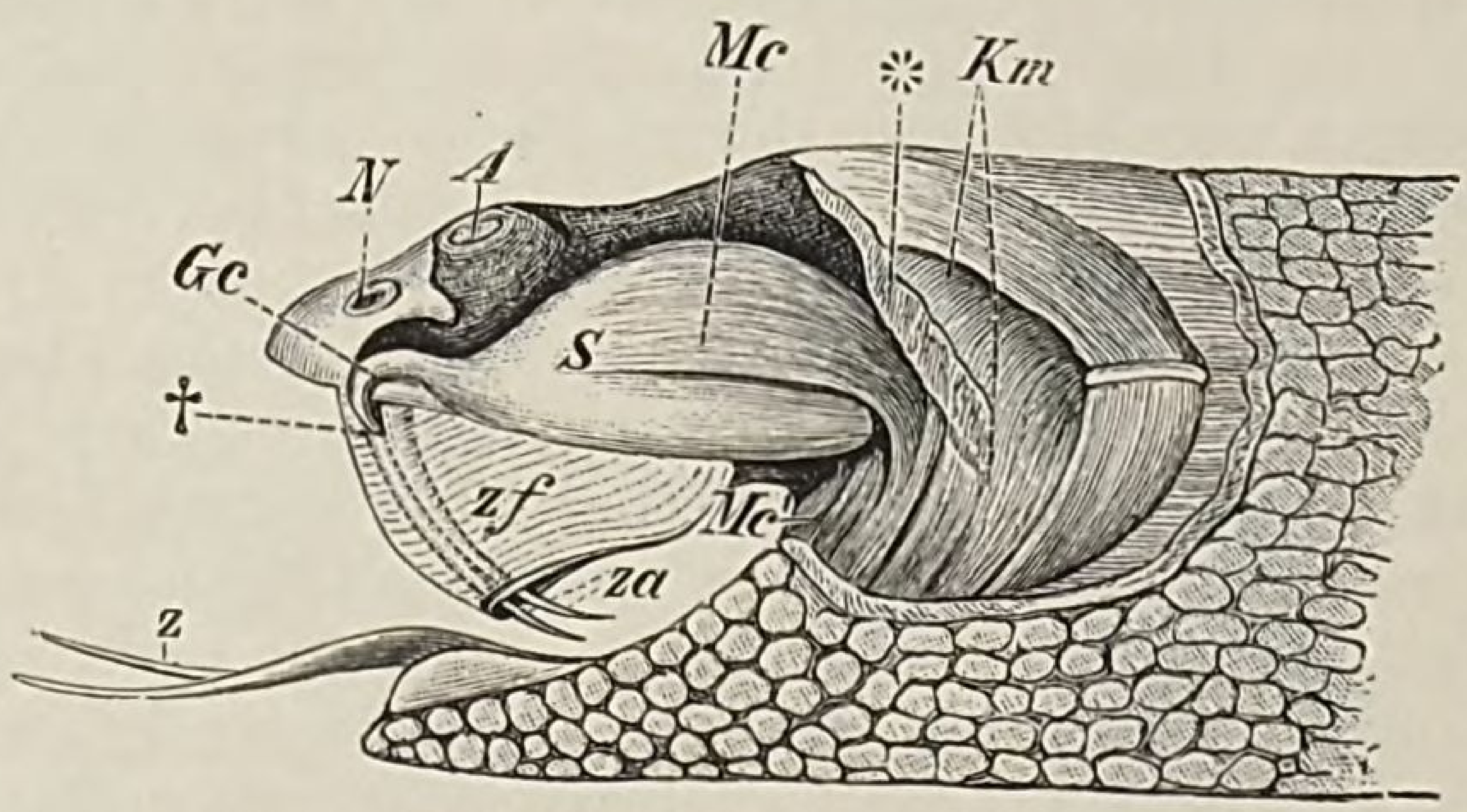


FIG. 950.—Poison apparatus of **Rattlesnake.** *A*, eye; *Gc*, poison-duct entering the poison-fang at †; *Km*, musles of mastication partly cut through at *; *Mc*. constrictor muscle; *Mc'*. continuation of the constrictor muscle to the lower jaw; *N*. nasal opening; *S*, fibrous poison-sac; *Z*, tongue; *Za*, opening of the poison-duct; *Zf*, pouch of mucous membrane enclosing the poison-fangs. (From Wiedersheim.)

case of the venom of some kinds of Snakes, paralysis. According to the amount of the poison injected (in relation to the size of the animal) and the degree of its virulence (which differs not only in different kinds of Snakes, but in the same Snake under different conditions) the symptoms may result in death, or the bitten animal may recover. The poison is a clear, slightly straw-coloured or greenish liquid; it preserves its venomous properties for an indefinite period, even if completely desiccated. The poisonous principles are certain proteids not to be distinguished chemically from other proteids which have no such poisonous properties. Immunity against the effects of the poison, and relief of the symptoms after a bite has been inflicted, have been found to be conferred by injections of the serum of animals which have been treated with injections of increasing doses of the poison.

The majority of Snakes are viviparous. Some, however, lay

eggs, which, nearly always, like those of the oviparous Lizards, are left to be hatched by the heat of the sun, some of the Pythons being exceptional in incubating them among the folds of the body.

Hatteria lives in burrows in company with Shearwaters (*Puffinus*), and feeds on Insects and small Birds. It lays eggs enclosed in a tough, parchment-like shell.

Of the Chelonia some (Land-Tortoises) are terrestrial; others (Fresh-water Tortoises) inhabit streams and ponds, while the Sea-Turtles and Luths inhabit the sea. Even among Reptiles they are remarkable for their tenacity of life, and will live for a long time after severe mutilations, even after the removal of the brain; but they readily succumb to the effects of cold. Like most other Reptiles the Land and Fresh-water Tortoises living in colder regions hibernate in the winter; in warmer latitudes they sometimes pass through a similar period of quiescence in the dry season. The food of the Green Turtles is exclusively vegetable; some of the Land Tortoises are also exclusively vegetable feeders; other Chelonia either live on plant food, together with Worms, Insects, and the like, or are completely carnivorous. All are oviparous, the number of eggs laid being usually very great (as many as 240 in the Sea-Turtles); these they lay in a burrow carefully prepared in the earth, or, in the case of the Sea-Turtles, in the sand of the sea-shore, and having covered them over, leave them to hatch.

The Crocodiles and Alligators, the largest of living Reptiles, are in the main aquatic in their habits, inhabiting rivers, and, in the case of some species, estuaries. Endowed with great muscular power, these Reptiles are able, by the movements of the powerful tail and the webbed hind-feet, to dart through the water with lightning-like rapidity. By lying in wait motionless, sometimes completely submerged with the exception of the extremity of the snout bearing the nostrils, they are often able by the suddenness and swiftness of their onset to seize the most watchful and timid animals. In the majority of cases the greater part, and in some the whole, of their food consists of Fishes; but all the larger and more powerful kinds prey also on Birds and Mammals of all kinds, which they seize unawares when they come down to drink or attempt to cross the stream. On land their movements are comparatively slow and awkward, and they are correspondingly more timid and helpless.

The Crocodilia are all oviparous, and the eggs, as large in some species as those of a Goose, are brought forth in great numbers (sometimes 100 or more), and either buried in the sand, or deposited in rough nests.

Geographical Distribution.—The order Lacertilia, the most numerous of the orders of Reptiles living at the present day, is of very wide distribution, occurring in all parts of the earth's surface

except the circum-polar regions; but some of its larger sections are of limited range. The Geckos are numerous in all warm countries, their headquarters being Australia and the Oriental region. The snake-like Pygopidæ are entirely confined to the Australian region. The Agamidæ (a family which includes the Flying Lizards besides many others) are most abundantly represented in the Australian region, though extending to other regions of the Old World, except New Zealand and Madagascar. Of the Iguanas two genera occur in Madagascar and one in the Friendly Islands; all the other members of this group, which is a large one, are confined to America. Three families occur exclusively in America —the Xenosauridæ, the Teiidæ, and the Helodermidæ or poisonous Lizards. The Zonuridæ or Girdle-tailed Lizards are confined to Africa and Madagascar. The Anguidæ or Blind-worm Lizards are mostly American, but are represented in Europe and Asia. The family of the Monitors is distributed in Africa, Southern Asia, Oceania, and the Australian region. The snake-like Amphisbænians are most numerous in America, but are well represented in Africa, and occur also in the Mediterranean area. The Lacertidæ are most abundant in Africa, but occur in Europe and Asia. The family of the Skinks (Scincidæ) is of world-wide range, but is most abundant in Australia, Oceania, the Oriental region and Africa. Hatteria is confined to the New Zealand region, and at the present day only occurs on certain small islands off the N.E. coast and in Cook's Straits. The Chamæleons are most abundant in Africa and Madagascar, but there are representatives in various other parts of the Old World; they do not occur in the Australian, New Zealand, or Polynesian regions, and are only represented in Europe by one species which occurs in Andalusia.

Chelonia are widely distributed over the surface of the earth, by far the greater number being natives of tropical and temperate zones. The Sea-turtles, including the Hawk's bills and the Luths, are for the most part, but not entirely, confined to the tropical seas. Giant Land-tortoises occur, or occurred in historic times, on islands of the Galapagos and Mascarene groups.

Of the Crocodilia the Caimans are confined to Central and South America. The Alligators are represented in North America by one species and in China by another. The true Crocodiles occur widely distributed over Africa, Southern Asia, the northern parts of Australia and tropical America, while the Gavial occurs only in certain Indian and Burmese rivers.

Geological Distribution.—The Squamata are geologically the most recent of the existing orders of Reptiles. The earliest fossil remains of Lizards have been found in beds belonging to the Jurassic and Cretaceous periods; but most of the families are not represented earlier than the Tertiary. All the known fossil remains of Snakes, except one imperfectly known form from the

Cretaceous, have been found in deposits of Tertiary age. The Rhynchocephalia are much more ancient, being represented in deposits as old as the Permian by a genus—Palæohatteria—which, though differing in some respects from the living Hatteria, is sufficiently near it to be looked upon as a member of the same order: and other extinct Rhynchocephalians have been found in Triassic and in Tertiary strata. The order Chelonia was represented from the Triassic period onwards. Of the extinct forms

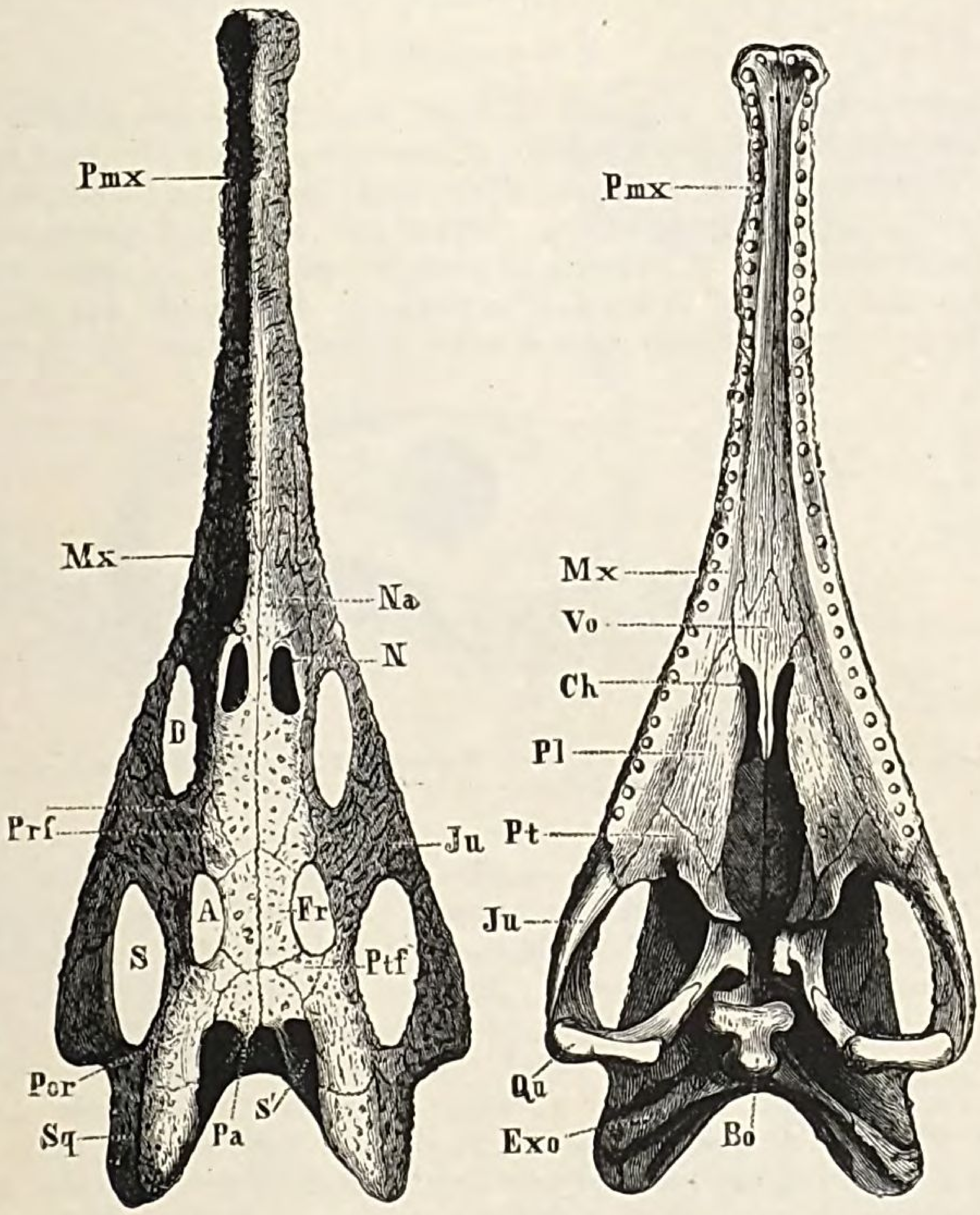


FIG. 951.—Skull of **Belodon.** A, from above; B, from below. *A*, orbit; *Bo*, basi-occipital; *Ch.* internal nares; *D*, pre-orbital fossa; *Exo.* exoccipital; *Fr.* frontal; *Ju.* jugal; *La.* lacrymal; *Mx.* maxilla; *Na.* nasal; *Pa.* parietal; *Pl.* palatine; *Pmx.* pre-maxilla; *Por.* post-orbital; *Prf.* pre-frontal; *Pt.* pterygoid; *Qu.* quadrate; *S*, lateral temporal fossa; *S'*, superior temporal fossa; *Sq.* squamosal; *Vo.* vomer. (From Zittel.)

one group—the *Athecata*—differs from the living Chelonia in having the carapace incompletely developed, entirely composed of dermal elements, and quite separate from the vertebræ and ribs. The Crocodilia date back as far as the Trias. The most primitive of the fossil forms (Fig. 951) had no palatine plates separating off a posterior nasal passage from the cavity of the mouth and had the external nares situated towards the middle of the snout. Later forms (post-Triassic) had palatine plates developed from the pre-

maxillæ, the maxillæ and the palatines; and some resembled the living members of the order in having such plates developed also from the pterygoids; all had the external nares situated towards the end of the snout. Those in which the palatine plates of the pterygoids were absent had usually amphicœlous vertebræ. Some of the fossil Crocodiles reached an immense size.

4. Extinct Groups of Reptiles.

Theromorpha.

The Theromorpha are a group of fossil Reptiles which exhibit remarkable points of resemblance to the Amphibia (Stegocephala), on the one hand, and to the lower Mammals on the other. They were lizard-like in shape, with limbs adapted for terrestrial locomotion. When the vertebral centra are complete, they are amphicœlous. A sternum is present, and also an episternum. There is a sacrum composed of from 2–6 vertebræ. Abdominal ribs are absent in most. The quadrate is firmly united with the other bones of the skull. The

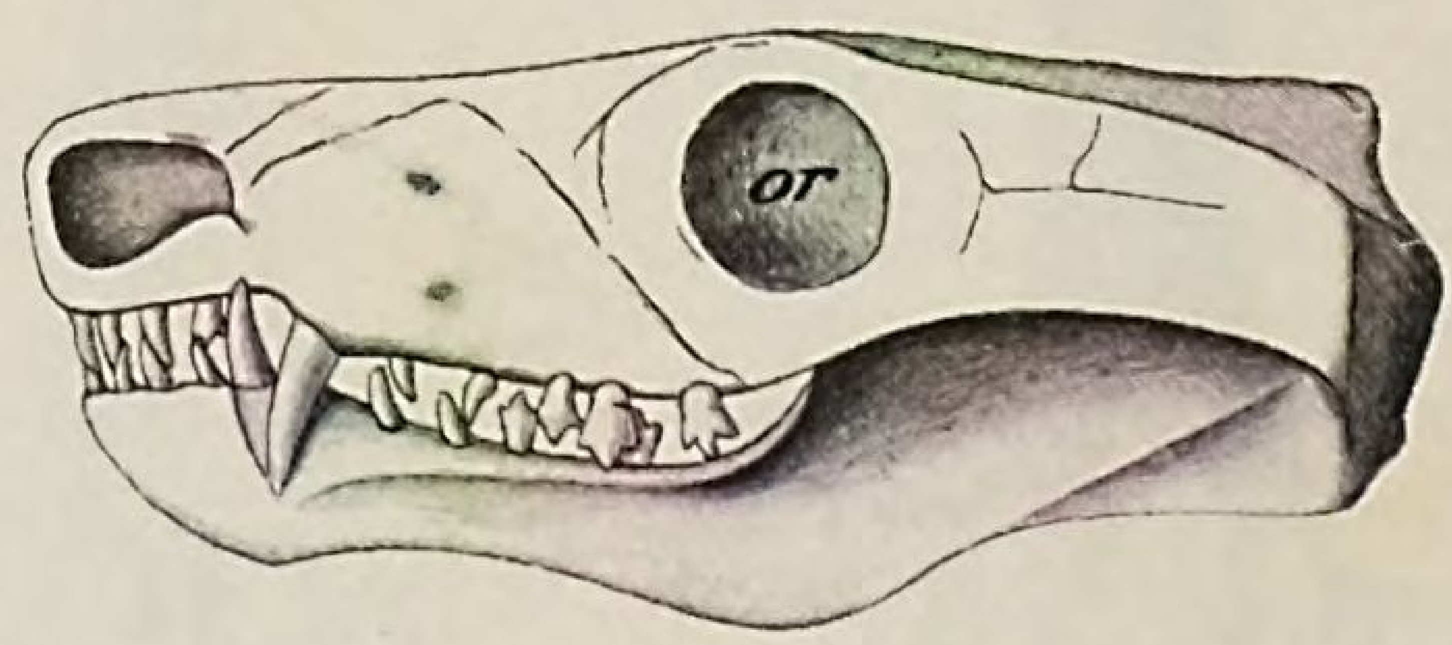


Fig. 952.—Left lateral aspect of the skull of **Galesaurus planiceps** *Or.* orbit. (After Nicholson and Lydekker.)

pre-maxilla is single; in some the maxillæ develop palatine plates. There is a parietal foramen, and sometimes one temporal arch is developed, sometimes two. The pterygoids meet in front of the basi-sphenoid, diverging anteriorly where the small palatines lie between them. In the pectoral arch there are clavicle, coracoid, pro-coracoid, and scapula, the last having a process—the acromion process—with which the pro-coracoid articulates. The pubes and ischia are closely united, and an obturator foramen is absent or extremely small. The teeth (Fig. 952) (which are not present in all) are thecodont, and in the higher forms bear a considerable resemblance to those of mammals in the regularity of their arrangement in sets, often with large *canines* or tusks. Palatine teeth are sometimes present. The Placodontia have remarkable broad crushing teeth on both upper and lower jaws and on the palate.

The Theromorpha only occur in beds of Permian and Triassic age, and have been found in South Africa and North America as well as Europe.

Sauropterygia.

The typical representatives of this order, such as the Plesiosaurs (Fig. 953), were aquatic Reptiles, sometimes of large size (up to 40 feet), though many were quite small. They had a lizard-like body, a very long neck, supporting a relatively small head, and a very short tail; the limbs were modified to form swimming-paddles. In older and less specialised members of the group, however, the limbs were not paddle-like, but adapted for walking.

The spinal column of the Sauropterygia is characterised by the great length

of the cervical, and the shortness of the caudal region. The vertebræ are amphicœlous. The sacrum consists of either one or two vertebræ. There is no sternum. In the skull there are large pre-maxillæ; the bony palate is absent; a transverse bone is present. The upper temporal arch alone is developed. There is a well-marked parietal foramen. The ring of bony plates (developed in the sclerotic) found in the orbit of some fossil Reptiles is not developed. The pectoral arch (Fig. 954) presents some remarkable features. The coracoids always

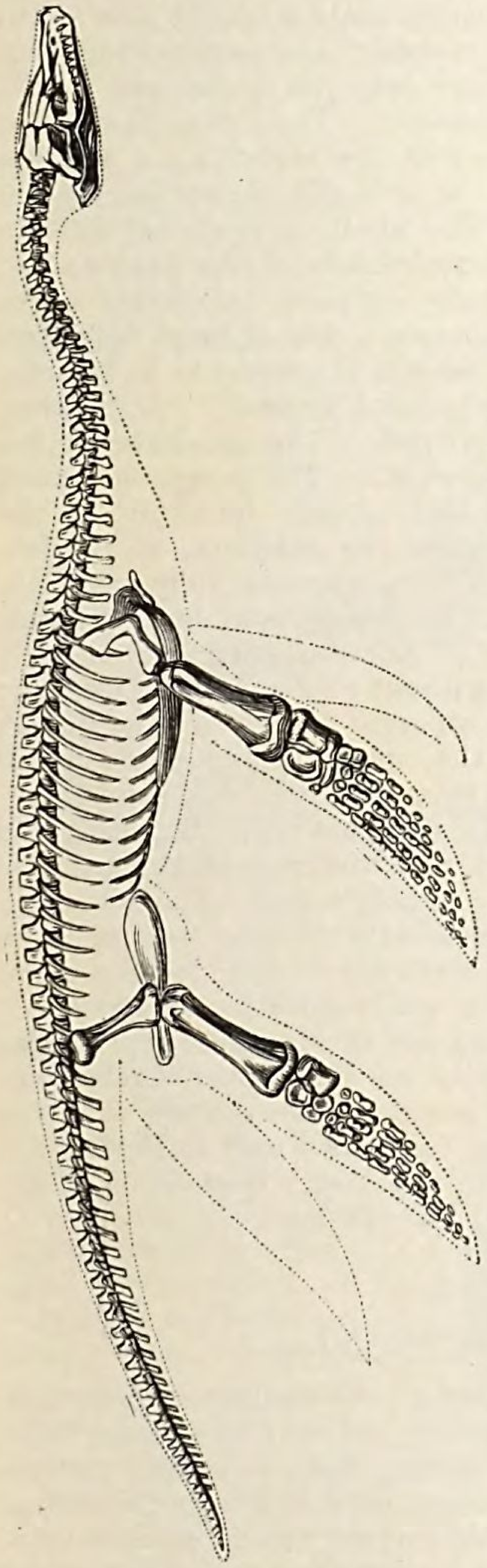


FIG. 953.—**Plesiosaurus macrocephalus.** Restored. (After Owen.)

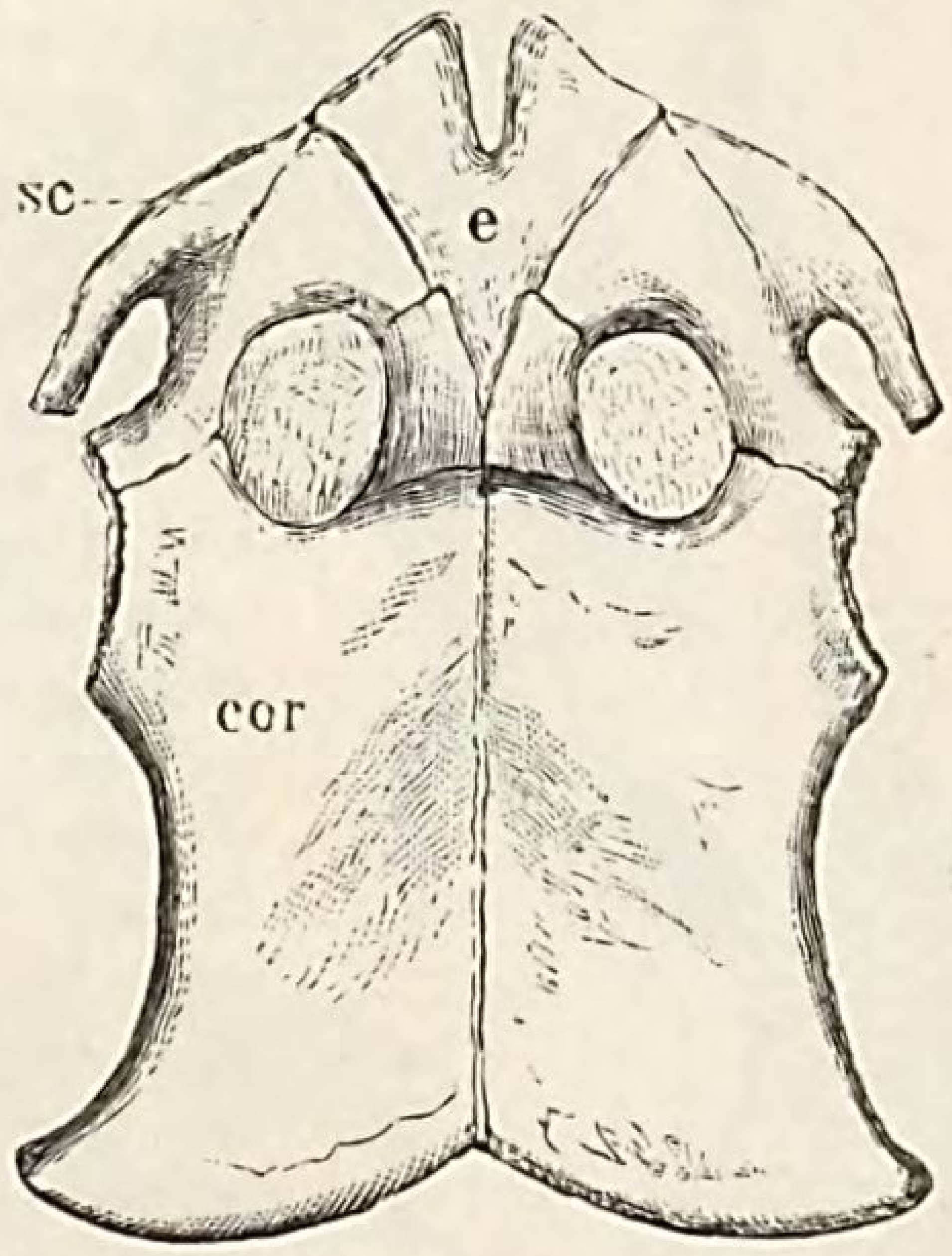


FIG. 954.—**Plesiosaurus,** pectoral arch. *cor.* coracoid; *e.* episternum; *gl.* glenoid cavity; *sc.* scapula. (After Zittel.)

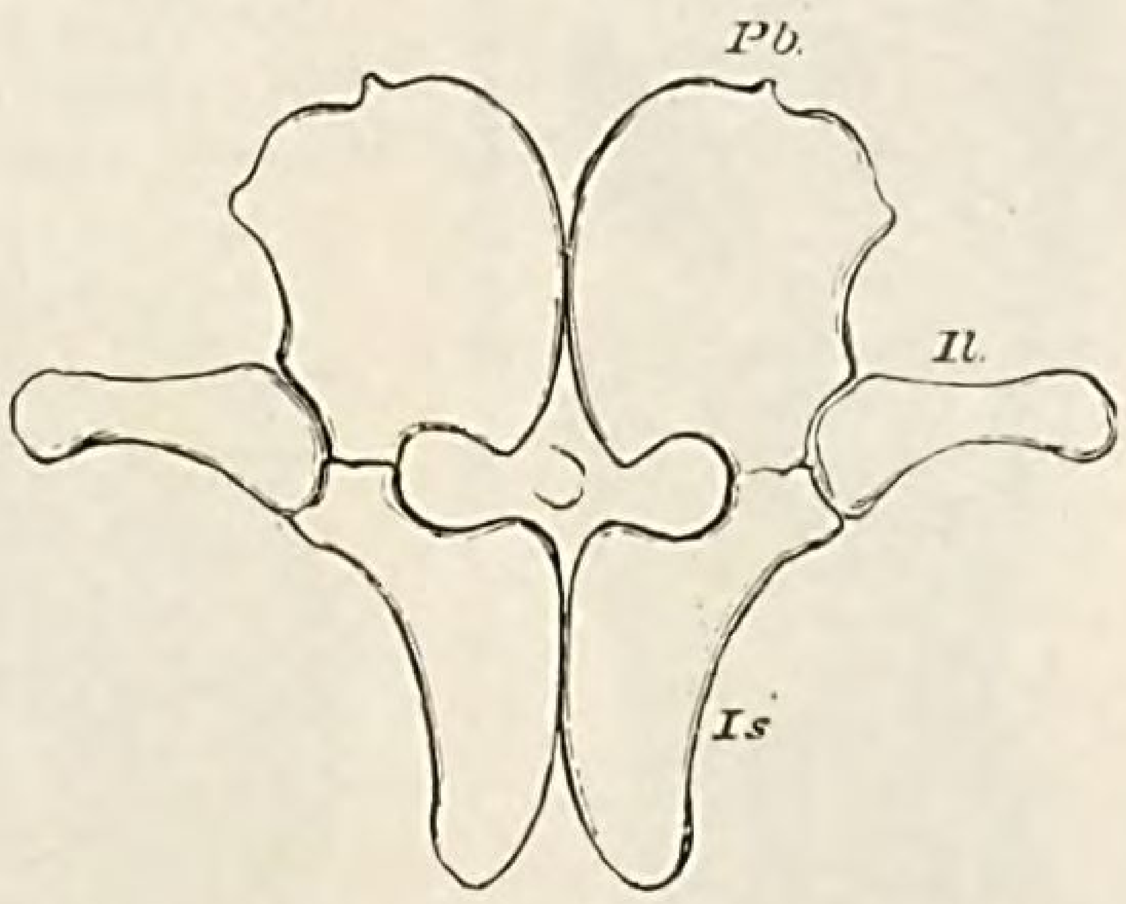


FIG. 955.—**Plesiosaurus,** pelvic arch. *Il.* ilium; *Is.* ischium; *Pb.* pubis. (After Huxley.)

meet in a ventral symphysis, and the ventral portions of the scapulæ may also meet. In front is, in most cases, an arch of bone, consisting of a median and two lateral portions, which probably represent the episternum and the clavicles: in some forms this is reduced or absent. An obturator foramen is sometimes, but not always, present in the pelvis (Fig. 955). The teeth are implanted in distinct sockets.

The Sauropterygia date back to the Trias, and perhaps to the Permian, extending onwards to the Cretaceous.

Ichthyopterygia.

The Ichthyopterygia, including Ichthyosaurus (Fig. 956) and its allies, were aquatic Reptiles, some of very large size (30 or 40 feet in length), with somewhat fish-like body, large head produced into an elongated snout, no neck, and an elongated tail, and with the limbs in the form of swimming-paddles. The vertebræ are amphicœlous. A sacrum is absent, so that only pre-caudal and caudal regions are distinguishable. The ribs have two heads for articulation with the vertebræ: a sternum is absent, but there is a highly developed system of abdominal ribs. The skull is produced into an elongated rostrum, formed chiefly of the pre-maxillæ, and with small nostrils situated far back. The orbits are large and contain a ring of bones developed in the sclerotic. A columella is present as in Lizards, and there is a large parietal foramen. Both temporal arches are developed. The quadrate is immovably fixed to the skull. The pterygoids meet in the middle line and extend forwards to the vomers, so as to separate the palatines, as in Hatteria. The pectoral arch contains only coracoid, scapula and clavicle, the pro-coracoid being absent. The coracoids are broad bones which meet ventrally for a short distance without overlapping. The bones of the pelvis are not strongly developed; the ilia are not connected with the spinal column; the pubes and ischia of opposite sides meet in ventral symphyses; but there is no obturator foramen. Humerus and femur are both short, and the rest of the bones of the limb are disc-like or polyhedral. The phalanges are numerous, and are usually in more, sometimes in fewer, than the usual five series. The teeth are not in separate sockets, but set in a continuous groove.



Fig. 956.—**Ichthyosaurus communis.** (After Owen.)

The Ichthyopterygia are of Mesozoic age, ranging from the Upper Trias to the Upper Cretaceous. Geographically their remains have a very wide distribution, having been found not only in Europe and North America, but in the Arctic Regions, in India, Africa, Australia, and New Zealand.

Dinosauria.

This order comprises a vast number of terrestrial Reptiles, some of gigantic size, of lizard-like or bird-like form, some approaching Birds in certain features of their structure, others coming nearer the earliest fossil Crocodiles. The surface was in some covered with a bony armour, sometimes armed with long spines. The fore- and hind-limbs were in some equally developed; in others the hind-limbs were much more powerful than the fore, and in many their structure appears adapted to a bipedal mode of progression (Fig. 957).

The centra are in general amphicœlous. The sacral region usually comprises 3 to 6 vertebræ. The thoracic ribs have double heads. Abdominal ribs are sometimes present. The sternum was incompletely ossified. The pre-maxillæ

are separate. In the pectoral arch the scapula is very large, the coracoid small, and the pro-coracoid absent. The pubis in some Dinosauria has a remarkable

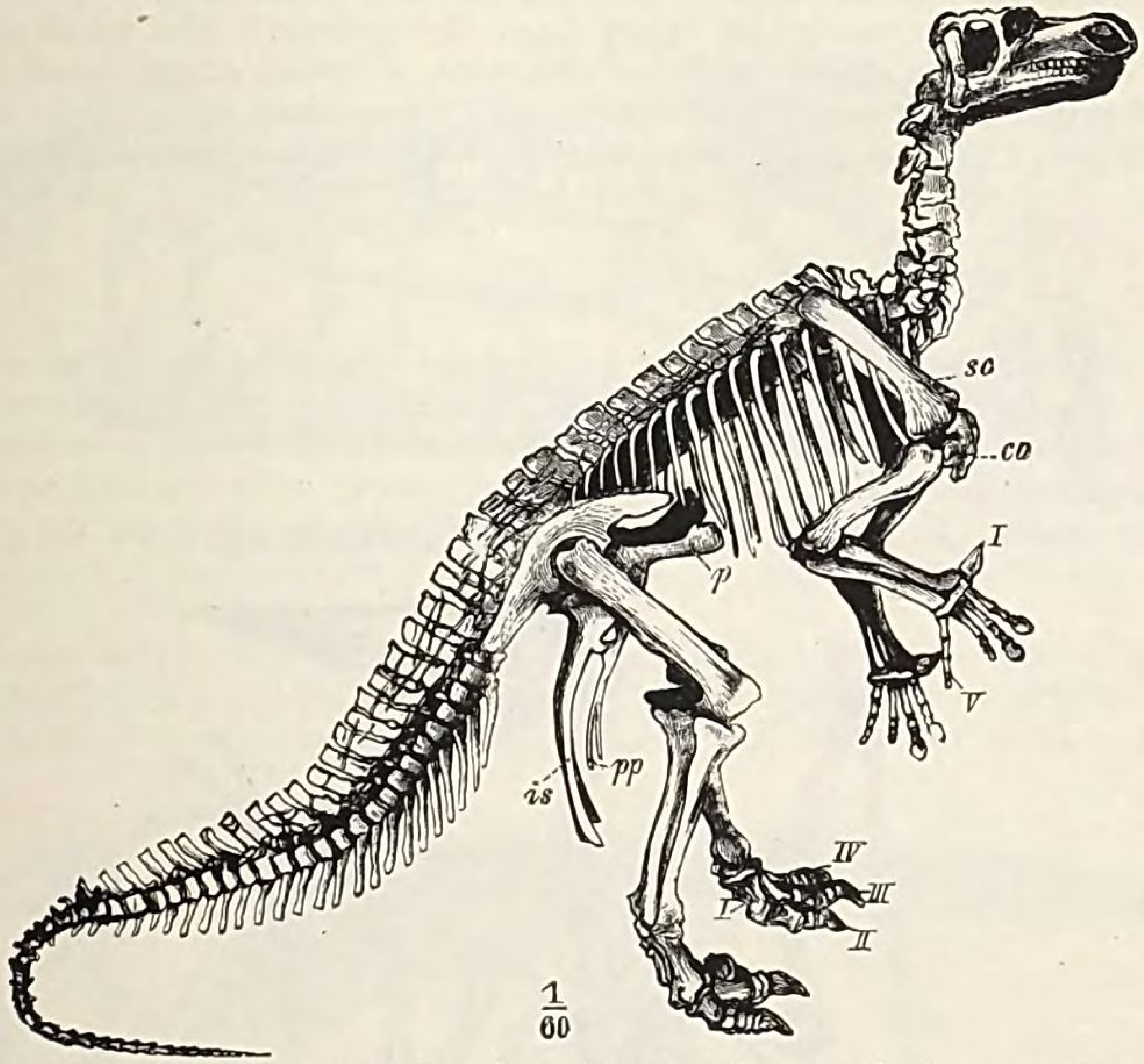


FIG. 957.—**Iguanodon bernissartensis.** One-sixtieth natural size. *co.* coracoid; *is.* ischium; *p.* pubis (pectineal process); *pp.* post-pubic process (pubis); *I—IV*, *I—V*, digits. (From Zittel, after Dollo.)

slender prolongation (Fig. 957, *pp.*) running downwards and backwards from the body of the bone parallel with the ischium, an arrangement not found elsewhere except in Birds; a pubic symphysis does not always occur. In certain points in the structure of the hind-limb itself some of the Dinosauria also bear a resemblance to Birds. The teeth, which are usually compressed and may have serrated edges, are sometimes placed in sockets, sometimes in grooves.

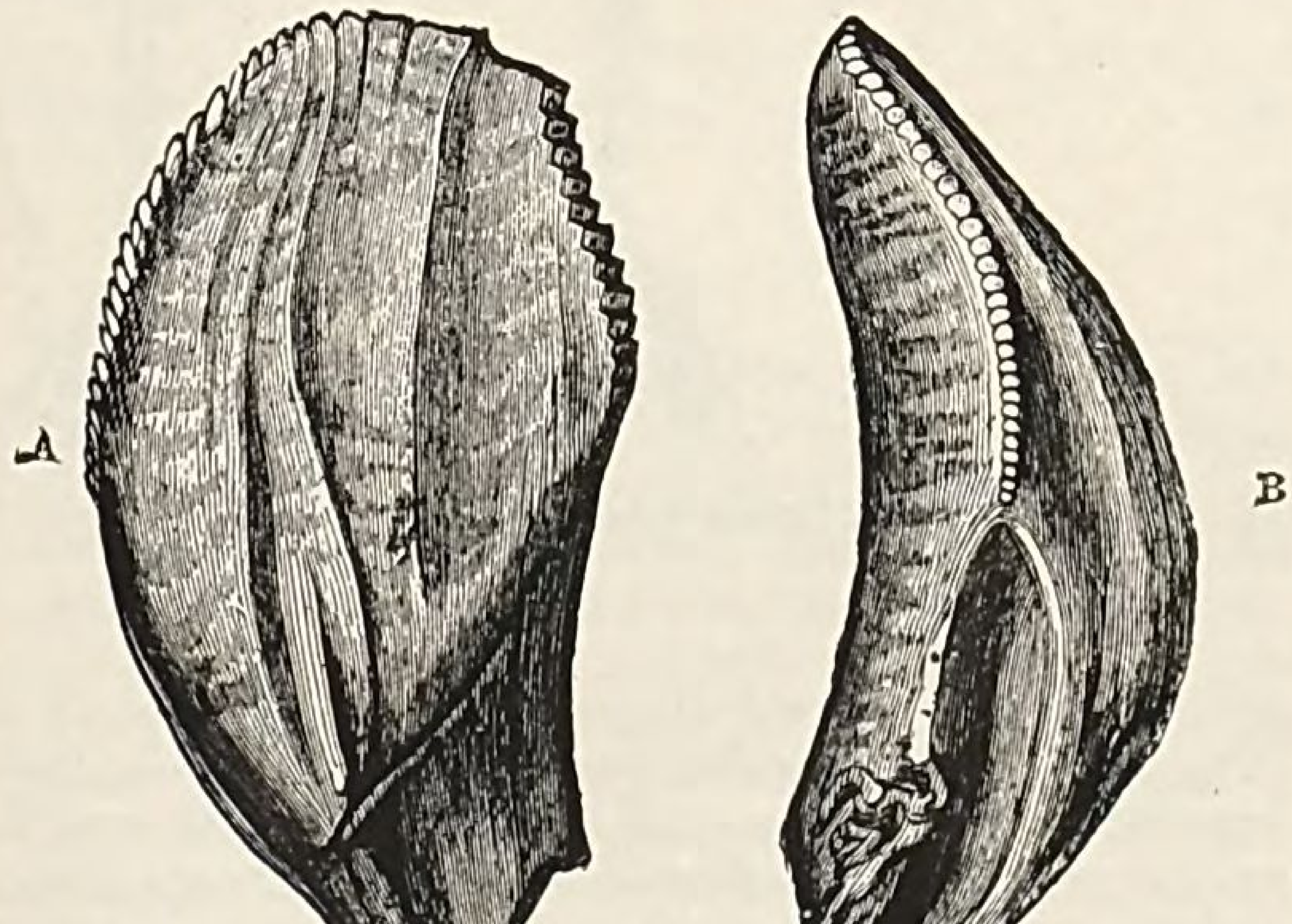


FIG. 958.—Teeth of **Iguanodon Mantelli.** *A*, from the inner, *B*, from the outer side. (From Zittel, after Mantell.)

Iguanodon (Fig. 957), one of the best-known genera, attains the length in the case of one species of over 30 feet. The limb-bones are hollow. The ischium and pubic process are long and slender, and inclined backwards and downwards parallel to one another. The hind-foot was *digitigrade*, *i.e.* the weight was supported on the phalanges of the three digits, and the elongated meta-

tarsals, which were immovably fixed, had a nearly vertical position as in Birds; the fore-limbs are relatively small, and fossil footprints that have been found indicate that the animal supported itself habitually in a half-erect posture like a Kangaroo, with the fore-limbs raised from the ground. The teeth (Fig. 958) are of a remarkable shape, flattened and with serrated edges, sometimes with vertical ridges which may be serrated. The Dinosauria range from the Trias to the Upper Cretaceous, and were most abundant in the Jurassic and Wealden.

PTEROSAURIA.

The Pterosauria or Pterodactyles are perhaps even more remarkable modifications of the reptilian type than any of the orders that have been hitherto alluded to. The chief peculiarities in the structure of these Reptiles were associated with a flying mode of locomotion, the organs of flight being, as in the Bird and the Bat, the fore-limbs. In the Pterodactyles (Fig. 959) the last digit on the ulnar side

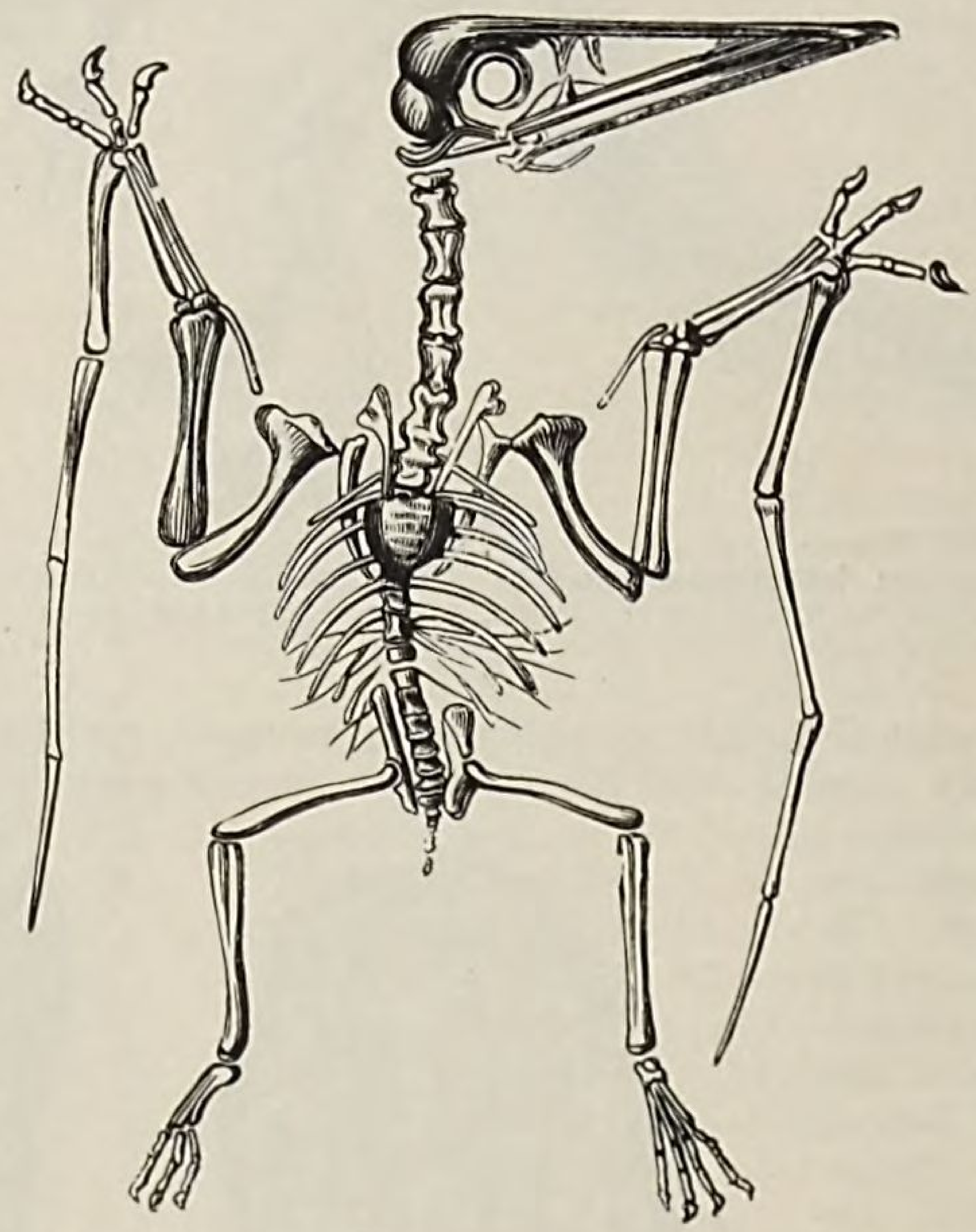


FIG. 959.—**Pterodactylus spectabilis.** Three-fourths of the natural size. (From Zittel, after H. v. Mayer.)

of the manus is enormously prolonged and thickened, and supported a web of skin (Fig. 961) which extended backwards to the hind-limbs and the tail. Most of the bones are hollow, and have pneumatic foramina as in Birds (p. 366). The vertebræ are procœlous, except the caudals, which are amphicœlous. The cervical vertebræ are elongated and stout, the neck being of considerable length; there are three to six anchylosed sacrals. The sternum is broad, with a longitudinal keel. The skull (Fig. 960), set on the neck at right angles as in a Bird, is of large size and resembles that of a Bird in general shape, and particularly in the presence of an elongated pointed rostrum; the orbits are large, and contain a ring of sclerotic ossifications. The sutures are obliterated as in the skull of a Bird. The quadrate is immovably fixed to the skull. In the pectoral arch the scapula and coracoid

are long and slender, like those of Birds. The pelvis and hind-limbs are weak as compared with the fore-limbs, and the pelvis does not exhibit any resemblance to that of Birds. The astragalus sometimes unites with the

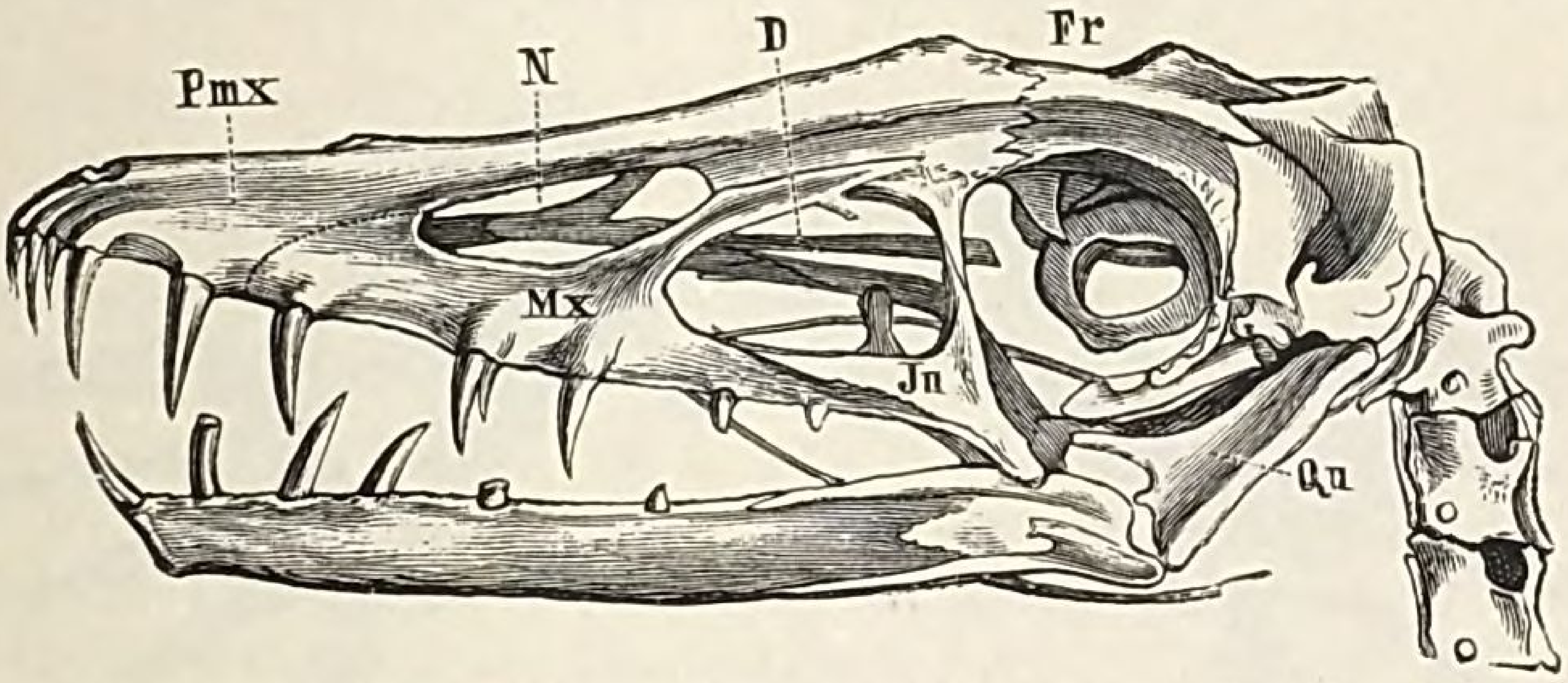


FIG. 960.—Skull of **Schaphognathus.** *D*, pre-orbital aperture; *Fr.* frontal; *Ju.* jugal; *Mx.* maxilla; *N.* nasal opening; *P. mx.* pre-maxilla; *Qu.* quadrate. (After Zittel.)

tibia. There is no trace of any exoskeleton. The brain, as shown by casts of the interior of the skull, bore interesting resemblances to that of Birds in the relations of the cerebellum and optic lobes, the latter being separated

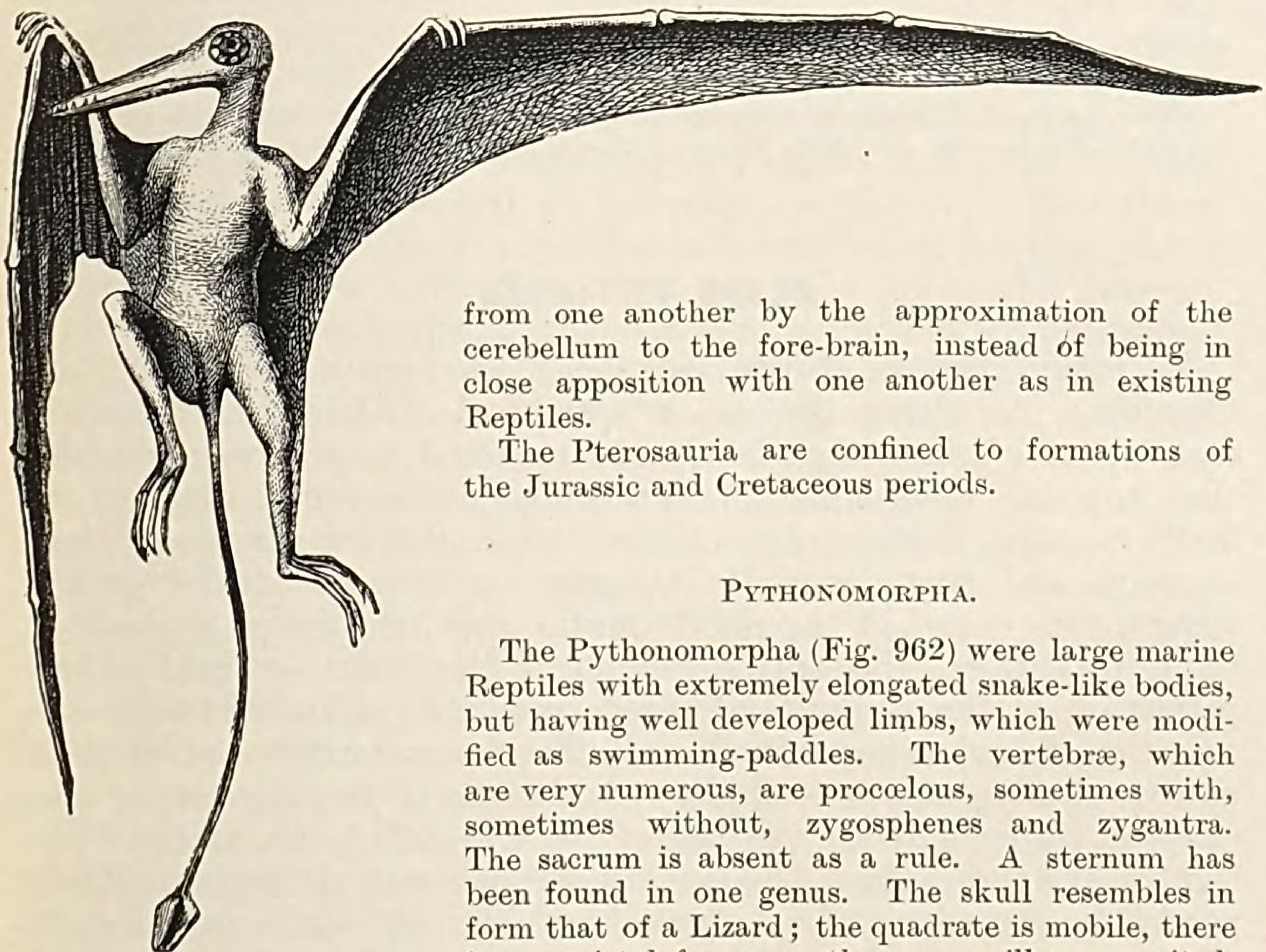


FIG. 961.—**Rhamphorhynchus,** restored. (After Zittel.)

from one another by the approximation of the cerebellum to the fore-brain, instead of being in close apposition with one another as in existing Reptiles.

The Pterosauria are confined to formations of the Jurassic and Cretaceous periods.

PYTHONOMORPHA.

The Pythonomorpha (Fig. 962) were large marine Reptiles with extremely elongated snake-like bodies, but having well developed limbs, which were modified as swimming-paddles. The vertebræ, which are very numerous, are procœlous, sometimes with, sometimes without, zygosphenes and zygantra. The sacrum is absent as a rule. A sternum has been found in one genus. The skull resembles in form that of a Lizard; the quadrate is mobile, there is a parietal foramen; the pre-maxillæ are united. There is only the supra-temporal arch. A peculiar feature is that the *supra-temporal* or *mastoid* serves to suspend the quadrate. The rami of the mandible are united by ligament at the symphysis. The pectoral arch comprises discoidal coracoids which meet ventrally, and a scapula which resembles that of the Rhynchocephalia: a clavicle is never present. In the

pelvis the ilium, which usually does not articulate with the spinal column, is a rod-shaped bone: the ischium and pubis resemble those of the Lizards. The bones of both fore- and hind-limbs are short; there are five digits in each. The teeth are conical, pointed, and anchylosed by expanded bases to the

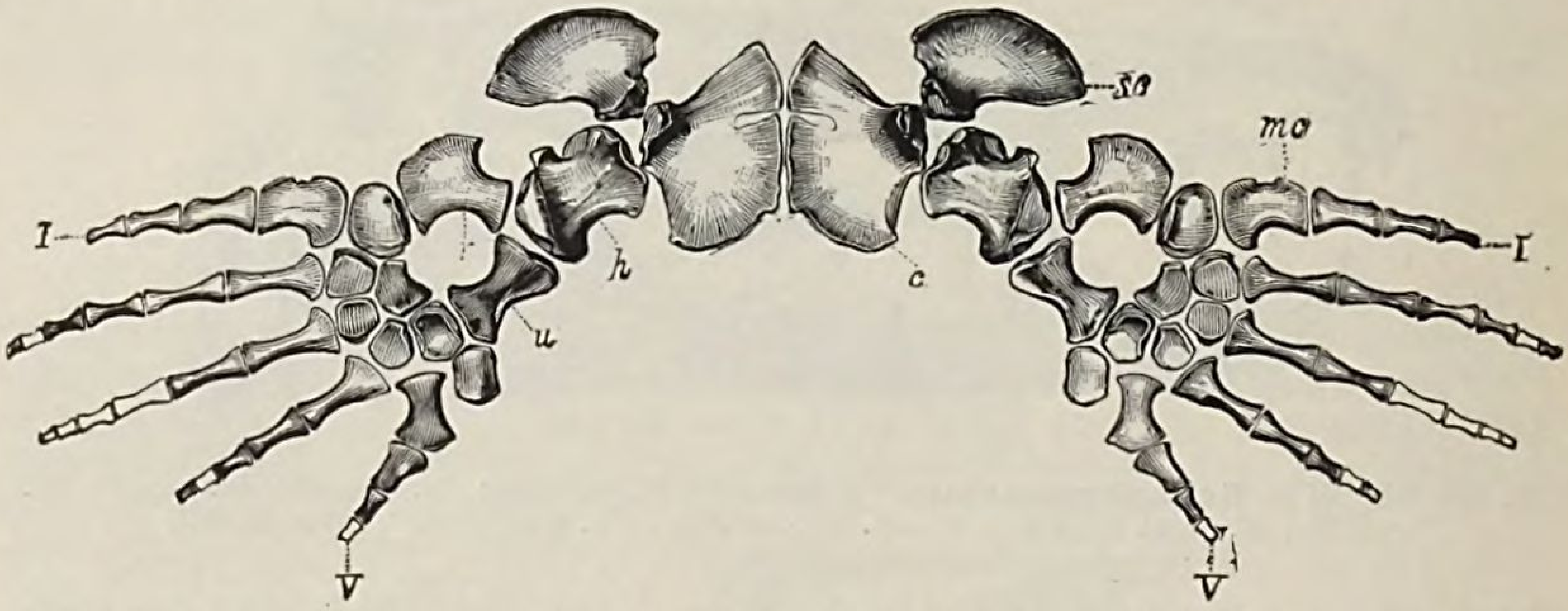


FIG. 962.—**Edestosaurus** (Pythonomorpha). Pectoral arch and fore-limbs. *c.* coracoid; *h.* humerus; *mc.* metacarpus; *r.* radius; *sc.* scapula; *u.* ulna; *I*, first digit; *V*, fifth digit. (From Zittel, after Marsh.)

summits of the maxillæ and pterygoids. Dermal scutes have been observed in one genus.

The remains of Pythonomorpha have been found only in certain beds belonging to the Cretaceous period in Europe, North America, and New Zealand.

CLASS VI.—AVES.

In many respects Birds are the most highly specialised of Craniata. As a class they are adapted for aërial life; and almost every part of their organisation is modified in accordance with the unusual environment. The non-conducting covering of feathers; the modification of the fore-limbs as wings, of the sternum and shoulder-girdle to serve as origins of the great wing muscles, and of the pelvic girdle and hind-limbs to enable them to support the entire weight of the body on land; the perfection of the respiratory system, producing a higher temperature than in any other animals; all these peculiarities are of the nature of adaptations to flight. Add to them the absence, in all existing Birds, of teeth, the loss of the left aortic arch, and of the right ovary and oviduct, the specialised character of the brain, the poorly developed olfactory organs, and the extraordinarily large and perfect eyes, and we have a series of strongly-marked characteristics such as distinguish hardly any other class. Moreover, the organisation of existing Birds is, in its essential features, singularly uniform, the entire class presenting less diversity of structure than many single orders of Fishes, Amphibians, and Reptiles.

1. Example of the Class.—The Common Pigeon (*Columba livia, var. domestica*).

The Common or Domestic Pigeon is known under many varieties, which differ from one another in size, proportions, coloration, details in the arrangements of the feathers, and in many points of internal anatomy. The Pouters, Carriers, Fantails, and Tumblers may be mentioned as illustrating extreme forms. All these varieties have, however, been produced by artificial selection, that is, by breeders selecting, generation after generation, the Birds which most nearly attained to some artificial standard of perfection, breeding from them alone, and killing off the inferior strains. The ancestral species from which the domestic breeds have in this way been evolved, is the Rock Pigeon (*Columba livia*) which is widely distributed in the Palæarctic and Oriental regions. The following description refers especially to the Common Dovecot Pigeon.

External Characters.—In the entire Bird (Fig. 963) the plump trunk appears to be continued insensibly into the small, mobile head, with its rounded brain-case and prominent *beak* formed of upper and lower jaws covered by horny sheaths. The head, neck, and trunk are invested in a close covering of *feathers*, all directed backwards and overlapping one another. Posteriorly the trunk gives origin to a number of outstanding feathers which constitute what is ordinarily called the tail. From the anterior region of the trunk spring the *wings*, also covered with feathers, and, in the position of rest, folded against the sides of the body. The legs spring from the hinder end of the trunk, but, owing to the thick covering of feathers, only the feet are to be seen in the living Bird, each covered with *scales* and terminating in four digits (*dg. 1′—dg. 4′*), three directed forwards and one backwards.

In order to make a fair comparison of the outer form with that of other craniate types it is necessary to remove the feathers. When this is done the Bird is seen to have a long, cylindrical, and very mobile neck, sharply separated both from head and trunk. The true tail is a short, conical projection of the trunk, known as the *uropygium*, and giving origin to the group of large feathers (*rct.*) to which the word "tail" is usually applied. On the dorsal surface of the uropygium is a papilla bearing on its summit the opening of a large gland, the *oil-gland* (*o.gl.*), used for lubricating or "preening" the feathers.

The wings show the three typical divisions of the fore-limb, upper arm, fore-arm, and hand, but the parts of the hand are closely bound together by skin, and only three imperfectly-marked digits, the second (*dg. 2*) much larger than the first (*dg. 1*) and third (*dg. 3*), can be distinguished. In the position of rest the

three divisions of the wing are bent upon one another in the form of a Z; during flight they are straightened out and extended so that the axis of the entire wing is at right angles to that of the trunk. On the anterior or preaxial border of the limb a fold of skin stretches between the upper-arm and the fore-arm; it is the *alar membrane* or *pre-patagium* (*pr. ptgm.*) A similar but much

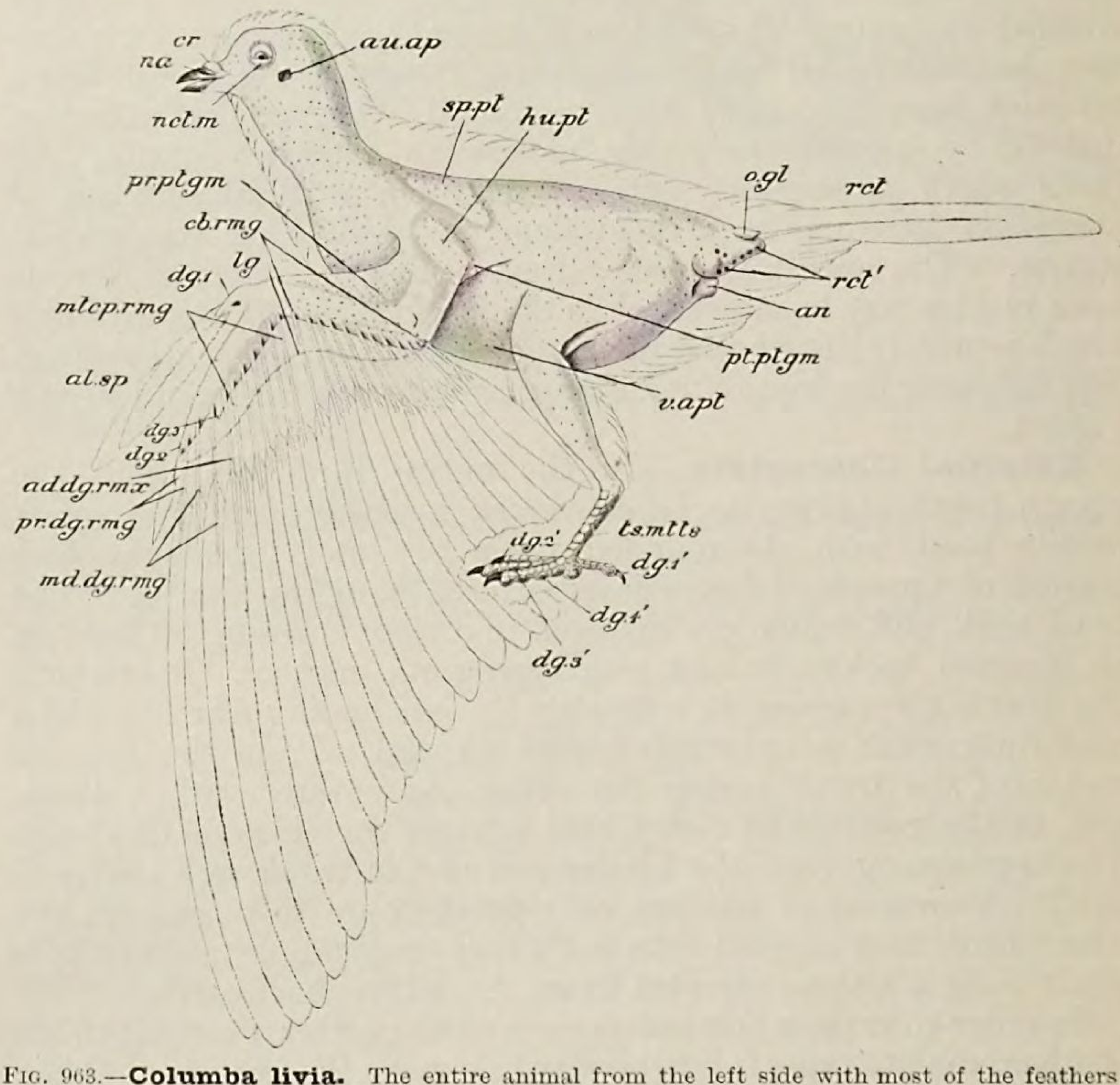


FIG. 963.—**Columba livia.** The entire animal from the left side with most of the feathers removed. *ad. dg. rmx.* ad-digital remex; *al. sp.* ala spuria; *an.* anus; *au. ap.* auditory aperture; *cb. rmg.* cubital remiges; *cr.* cere; *dg. 1, 2, 3,* digits of manus; *dg. 1', 2', 3', 4',* digits of pes; *hu. pt.* humeral pteryla; *lg.* ligament of remiges; *md. dg. rmg.* mid-digital remiges; *na.* nostril; *nct. m.* nictitating membrane; *o. gl.* oil-gland; *pr. dg. rmg.* pre-digital remiges; *pr. ptgm.* pre-patagium; *pt. ptgm.* post-patagium; *rct.* mesial rectrix of right side; *rct'.* sacs of left rectrices; *sp. pt.* spinal pteryla; *ts. mtts.* tarso-metatarsus; *v. apt.* ventral apterium

smaller fold extends, postaxially, between the proximal portion of the upper arm and the trunk; this is the *post-patagium* (*pt. ptgm.*).

In the hind-limb the short thigh is closely bound to the trunk, not standing well out as in a Reptile, but directed downwards and forwards; the long shank extends from the knee downwards and backwards; and the foot is clearly divisible into a proximal portion, the *tarso-metatarsus* (*ts. mtts.*), and four digits, of which one, the hallux (*dg. 1'*), is directed backwards, the others, the 2nd, 3rd, and

4th of the typical foot, forwards. The entire hind-limb is in a plane parallel with the sagittal plane of the trunk.

The mouth is terminal, and is guarded by the elongated upper and lower beaks; it has, therefore, a very wide gape. On each side of the base of the upper beak is a swollen area of soft skin, the *cere* (*cr.*) surrounding the *nostril* (*na.*), which has thus a remarkably backward position. The *eyes* are very large and each is guarded by an upper and a lower eyelid, and a transparent nictitating membrane (*nct. m.*). A short distance behind the eye is the *auditory aperture* (*au. ap.*), concealed by feathers in the entire Bird, and leading into a short external auditory meatus, closed below by the tympanic membrane. The *anus* or cloacal aperture (*an.*) is a large transversely elongated aperture placed on the ventral surface at the junction of the uropygium with the trunk.

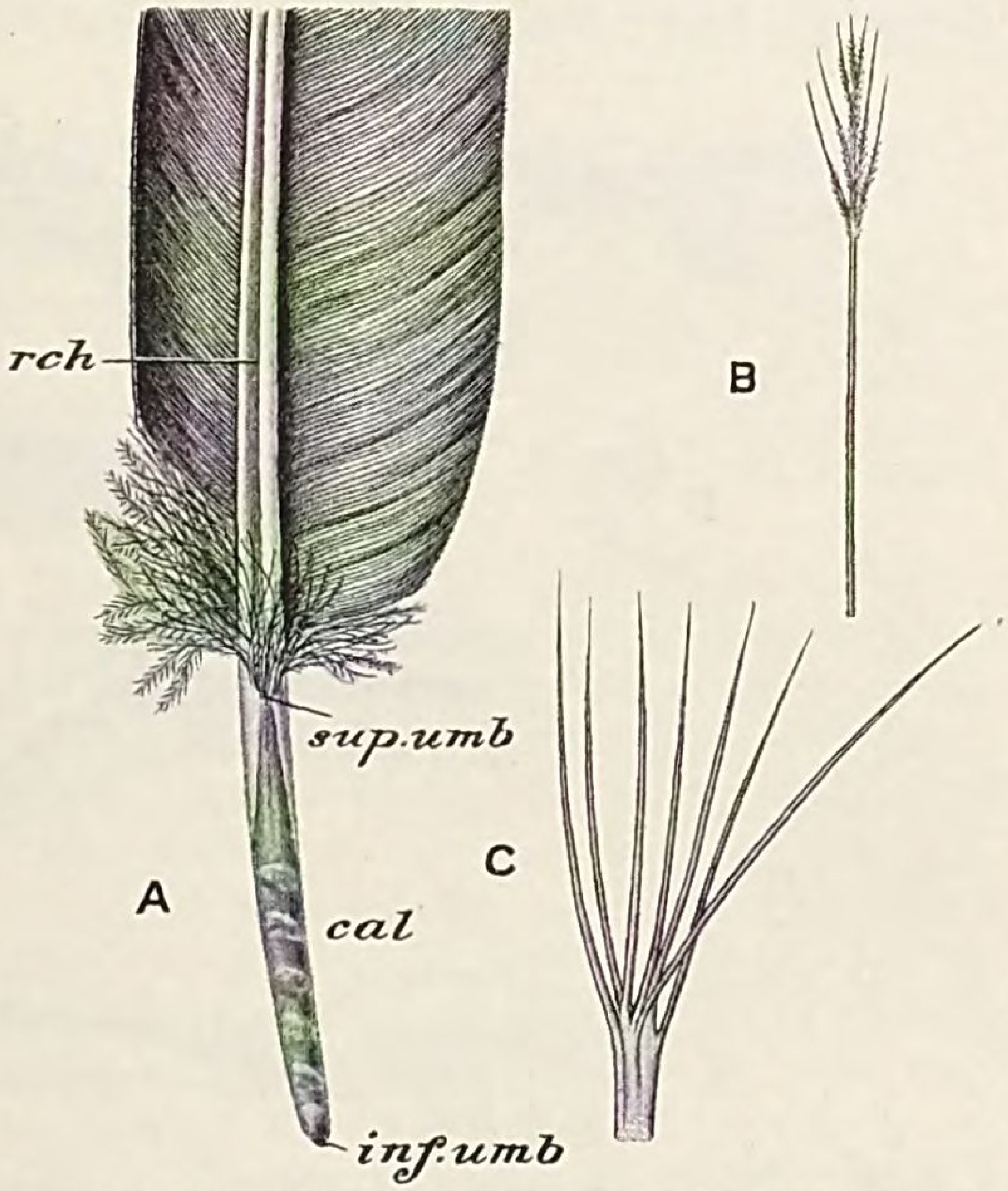


FIG. 964.—**Columba livia.** A, proximal portion of a remex; *cal.* calamus; *inf. umb.* inferior umbilicus; *rch.* rachis; *sup. umb.* superior umbilicus. B, filoplume. C, nestling-down. (C, from Bronn's *Thierreich.*)

Exoskeleton. — The exoskeleton is purely epidermal, like that of the Lizard, which it also resembles in consisting partly of horny *scales*. These cover the tarso-metatarsus and the digits of the foot and are quite reptilian in appearance and structure. Each digit of the foot is terminated by a *claw* which is also a horny product of the epidermis, and the *beaks* are of the same nature. The rest of the body, however, is covered by *feathers*, a unique type of epidermal product found nowhere outside the present class.

A feather (Fig. 964) is an elongated structure consisting of a hollow stalk, the *calamus* or quill (*cal.*), and an expanded distal portion, the *vexillum* or vane. At the proximal end of the quill is a small aperture, the *inferior umbilicus* (*inf. umb.*), into which fits, in the entire Bird, a small conical prolongation of the skin, the

feather papilla. A second, extremely minute aperture, the *superior umbilicus* (*sup. umb.*), occurs at the junction of the quill with the vane on the inner or ventral face of the feather, *i.e.*, the face adjacent to the body. A small tuft of down in the neighbourhood of the superior umbilicus represents the *after-shaft* of many Birds, including some Pigeons (*vide infra*).

The vane has a longitudinal axis or *rachis* (*rch.*) continuous proximally with the quill, but differing from the latter in being solid. To each side of the rachis is attached a kind of membrane forming the expanded part of the feather and composed of *barbs*—delicate, thread-like structures which extend obliquely outwards

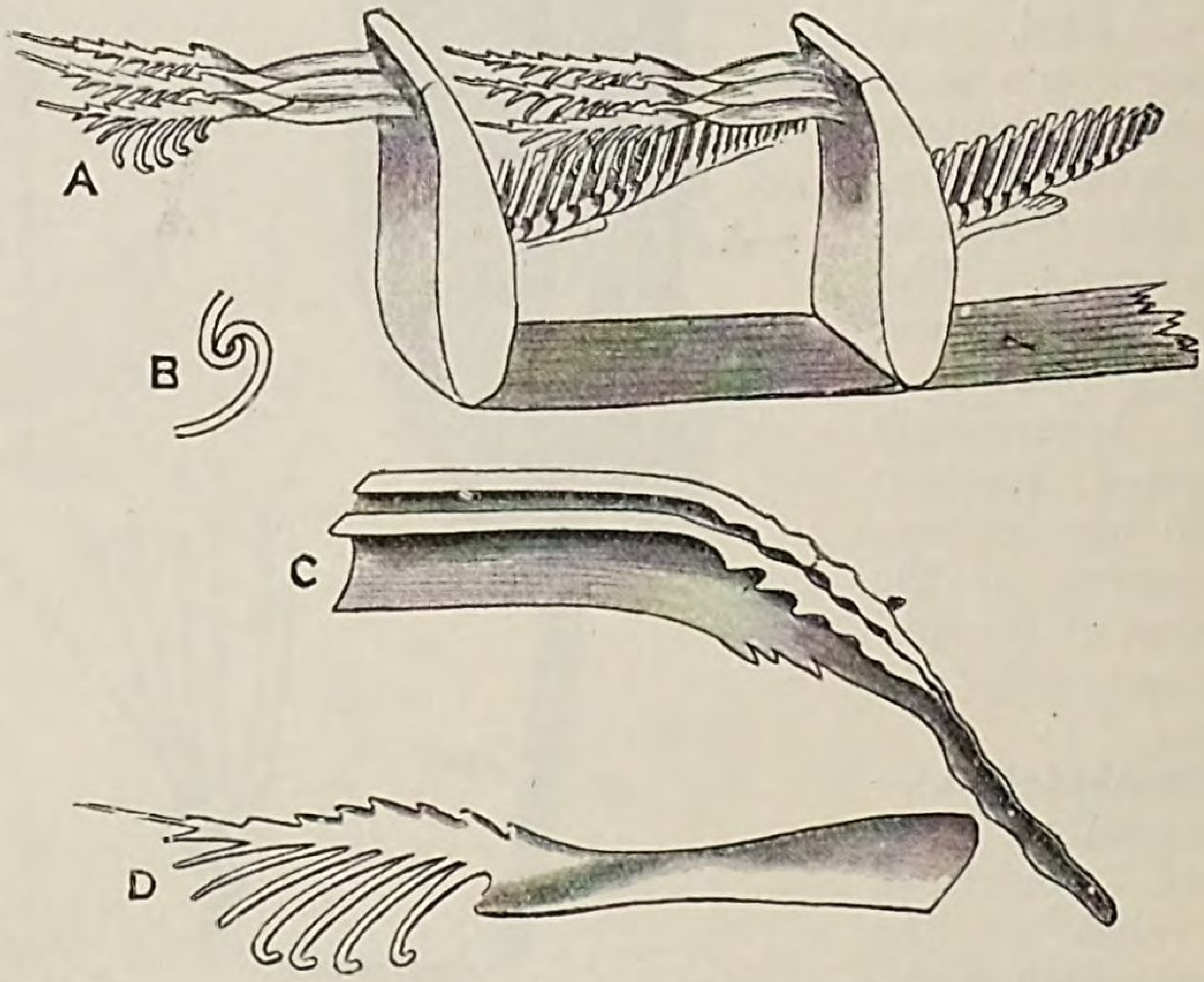


FIG. 965.—Structure of **Feather.** A, small portion of feather with pieces of two barbs, each having to the left three distal barbules, and to the right a number of proximal barbules, many of them belonging to adjacent barbs. B, Hooklet of distal barbule interlocking with flange of proximal barbule. C, two adjacent proximal barbules. D, a distal barbule. (From Headley, after Pycraft.)

from the rachis. In an uninjured feather the barbs are closely connected so as to form a continuous sheet, but a moderate amount of force separates them from one another, and it can readily be made out with the aid of a magnifying glass that they are bound together by extremely delicate oblique filaments, the *barbules*, having the same general relation to the barbs as the barbs themselves to the rachis.

The precise mode of interlocking of the barbs can be made out only by microscopic examination. Each barb (Fig. 965, A) is a very thin and long plate springing by a narrow base from the rachis, and pointed distally. From its upper edge—the edge

furthest from the body of the Bird—spring two sets of barbules, a *proximal set* (C) directed towards the base of the feather, and a *distal set* (D) towards its tip. Owing to their oblique disposition the distal barbules of a given barb cross the proximal barbules of the next, each distal barbule being in contact with several proximal barbules of the barb immediately distal to it (A). The lower edge of the distal barbule is produced into minute *hooklets* (D): in the entire feather the hooklets of each distal barbule hook over prominent *flanges* of the proximal barbules with which it is in contact (A, B). In this way the parts of the feather are so bound together that the entire structure offers great resistance to the air.

Among the *contour feathers* which form the main covering of the Bird and have the structure just described, are found *filoplumes* (Fig. 964, B.), delicate, hair-like feathers having a long axis and a few barbs, devoid of locking apparatus, at the distal end. Nestling Pigeons are covered with a temporary investment of *down-feathers* (C), in which also there is no interlocking of the barbs: when these first appear each is covered by a horny sheath like a glove-finger.

Feathers, like scales, arise in the embryo from papillæ of the skin (Fig. 966, A, *Pap.*), formed of derm with an epidermal covering. The papilla becomes sunk in a sac, the *feather-follicle* (B, *F*), from which it subsequently protrudes as an elongated *feather-germ* (*F K*), its vascular dermal interior being the *feather-pulp* (*P*). The Malpighian layer of the distal part of the feather-germ proliferates in such a way as to form a number of vertical radiating ridges (C, *Fal SM'*): its proximal part becomes uniformly thickened, and in this way is produced the rudiment of a down-feather, having a number of barbs springing, at the same level, from the distal end of the quill. The horny layer of the epidermis (*H S* (*sc'*)) forms the temporary sheath which is thrown off as the feather grows and expands. The pulp of the permanent feather (D, *F'*) is formed from the lower or deep end of that of the down-feather, and its development is at first similar, but, instead of the ridges of the Malpighian layer remaining all of one size, two adjacent ones outgrow the rest and become the rachis; as the latter elongates it carries up with it the remaining ridges, which become the barbs.

The feathers do not spring uniformly from the whole surface of the body, but from certain defined areas (Fig. 967), the *feather tracts* or *pterylæ* (*sp. pt.*, *hu. pt.*, &c.), separated from one another by featherless spaces or *apteria* (*v. apt.*, &c.), from which only a few filoplumes grow. The feathers are, however, long enough to cover the apteria by their overlap, and the body is thus completely covered with a thick, very light, and non-conducting investment.

In the wings and tail certain special arrangements of the feathers are to be distinguished. When the wing is stretched out at right

angles to the trunk twenty-three large feathers (Fig. 963) are seen to spring from its hinder or post-axial border: these are the *remiges* or wing-quills. Twelve of them are connected with the ulna and are called *cubitals* or *secondaries* (*cb. rmg.*) The rest are known as *primaries*: seven of these are attached to the meta-

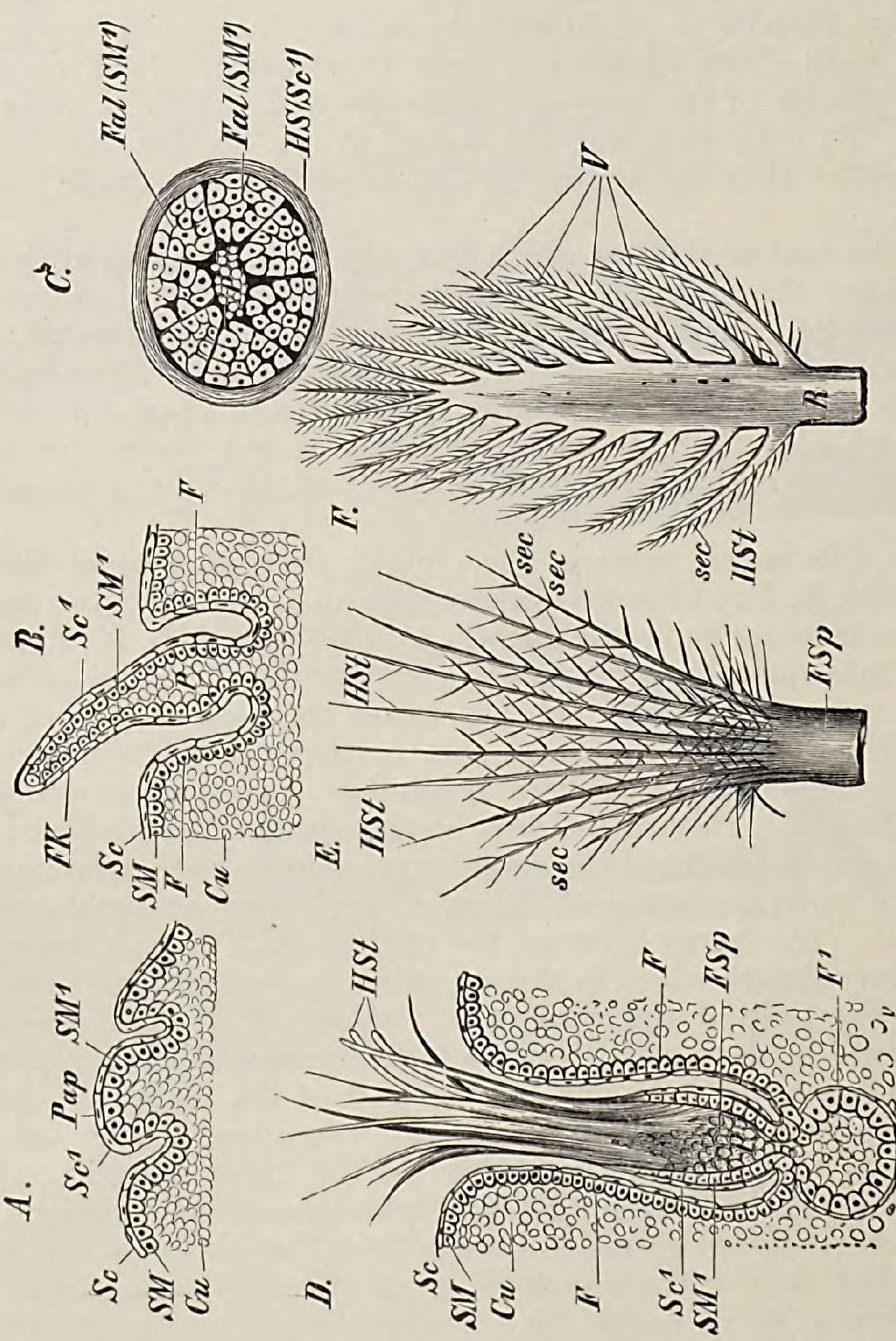


FIG. 966.—Six stages in the development of the feather. A, early feather-papilla in its follicle; B, feather-germ; C, transverse section of feather-germ; D, down-feather in its follicle; E, down-feather removed from follicle; F, early stage of permanent feather. *Cu*, dermis; *F*, follicle of down-feather; *F'*. follicle of permanent feather; *Fal.* (*SM'*.) folds of Malpighian layer extending into feather-germ; *FK*, feather-germ; *FSp*, calamus of down-feather; *HS*(Sc^1). feather-sheath; *H*, *St*, barbs; *P*. pulp; *Pap*. feather-papilla; *R*. rachis; *Sc*. stratum corneum; sc^1. its extension into feather-papilla; *sec*. barbules; *SM*. stratum Malpighii; *SM'*. its extension into feather-papilla; *V*. vexillum. (From Wiedersheim, after Studer.)

carpal region, and are hence called *metacarpals* (*mtcp. rmg.*), the remaining four or *digitals* to the phalanges of the second and third digits. These are again distinguished into a single *ad-digital* (*ad. dg. rmx.*) connected with the single phalanx of the third digit (Fig. 975, *ph.3*), two *mid-digitals* (*md. dg. rmg.*) with

the proximal phalanx of the second digit (Fig. 975, *ph.2*), and two *pre-digitals* (*pr. dg. rmg.*) with its distal phalanx (Fig. 975, *ph.2'*). A special tuft of feathers on the anterior border of the wing, arising from the pollex (Fig. 975, *ph.1*), forms the *ala spuria* (*al. sp.*). The spaces which would otherwise be left between the bases of the remiges are filled in, both above and below, by several rows of *upper* and *under wing-coverts.* In the tail there are twelve long *rectrices* (*rct.*) or tail-quills, springing in a semicircle from the uropygium; their bases are covered, as in the

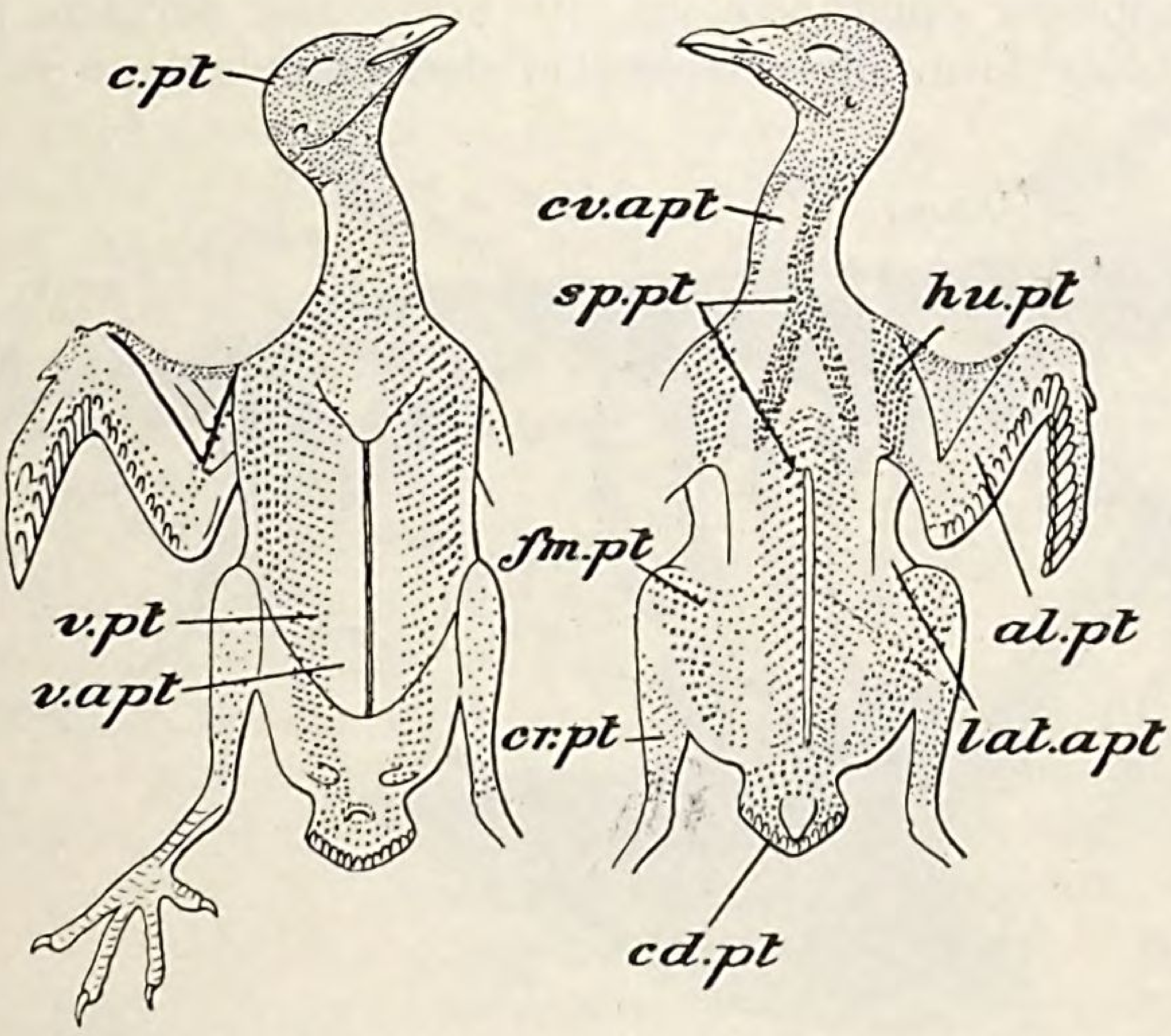


FIG. 967.—Pterylosis of **Columba livia.** A, ventral; B, dorsal. *al. pt.* alar pteryla or wing-tract; *c. pt.* cephalic pteryla or head-tract; *cd. pt.* caudal pteryla or tail-tract; *cr. pt.* crural pteryla; *cr. apt.* cervical apterium or neck-space; *fm. pt.* femoral pteryla; *hu. pt.* humeral pteryla; *lat. apt.* lateral apterium; *sp. pt.* spinal pteryla; *v. apt.* ventral apterium; *v. pt.* ventral pteryla. (After Nitsch.)

wing, by *upper* and *under tail-coverts.* The whole feather-arrangement is known as the *pterylosis.*

Endoskeleton.—The *vertebral column* is distinguished from that of most other Craniata by the great length and extreme mobility of the neck, the rigidity of the trunk-region, and the shortness of the tail. As in Reptilia, the cervical passes almost insensibly into the thoracic region, and the convention is again adopted of counting as the first thoracic (Fig. 968, *th. v. 1*), the first vertebra having its ribs united with the sternum. There are fourteen cervical vertebræ, the last two of which have double-headed ribs (*cv.r.*) each having its proximal end divisible into the *head* proper articulating with the centrum of the vertebra, and a *tubercle* with the transverse process: their distal ends are free, not uniting with the sternum. In the third to the twelfth there are vestigial

ribs (Fig. 969, *rb.*), each having its head fused with the centrum, and its tubercle with the transverse process. The whole rib thus has the appearance of a short, backwardly-directed transverse process perforated at its base; the perforation transmits the vertebral artery, and is called the *vertebrarterial foramen* (*vrb. f.*)

The centra of the cervical vertebræ differ from those of all other Vertebrata in having saddle-shaped surfaces, the anterior face (Fig. 969, A) being concave from side to side and convex from above downwards, the posterior face (B) convex from side to side and concave from above downwards. Thus the centrum in sagittal section appears opisthocœlous, in horizontal section procœlous. This peculiar form of vertebra is distinguished as *heterocœlous.*

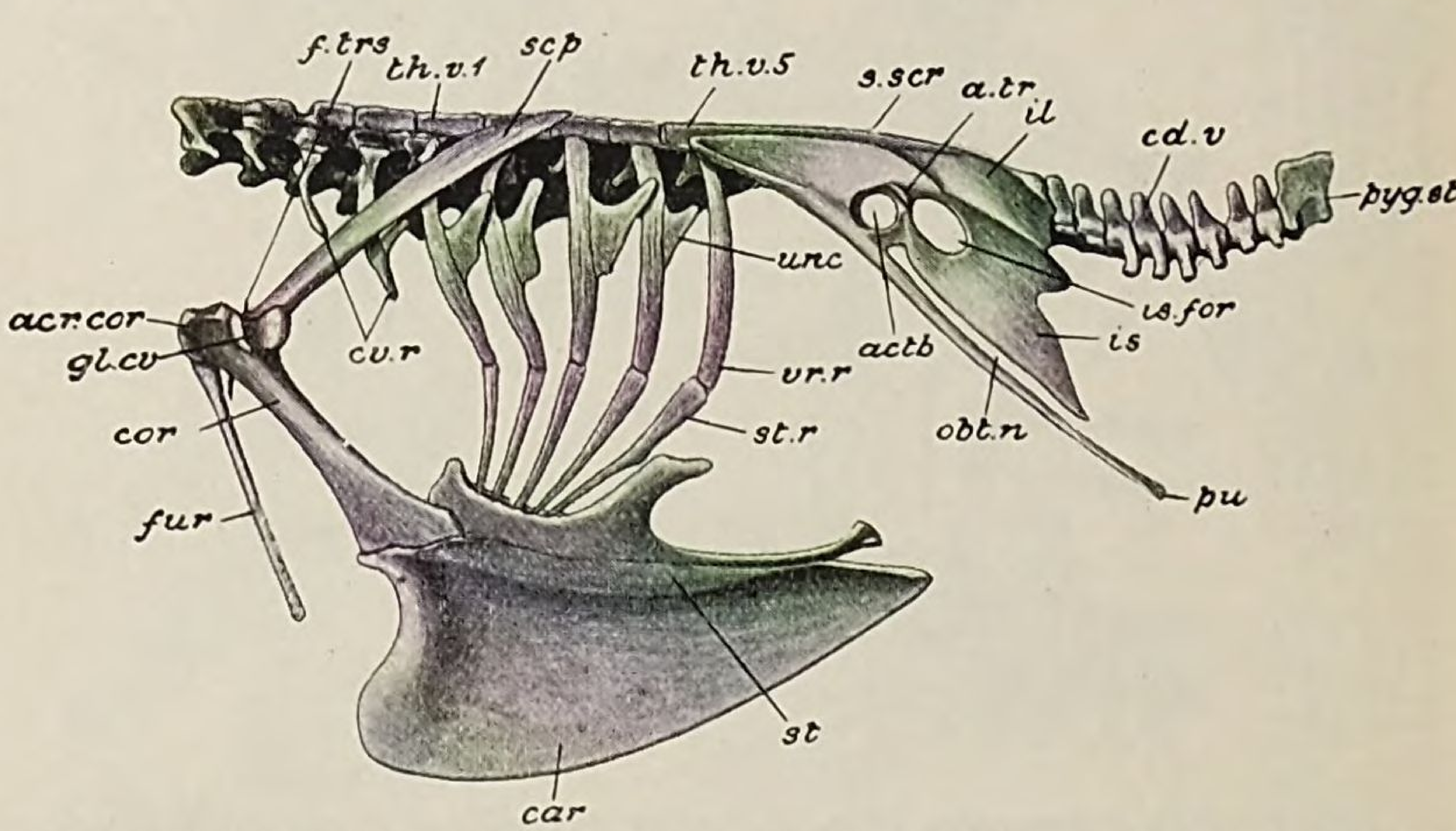


FIG. 968.—**Columba livia.** The bones of the trunk. *acr. cor.* acrocoracoid; *a.tr.* anti-trochanter; *actb.* acetabulum; *car.* carina sterni; *cd. v.* caudal vertebræ; *cor.* coracoid; *cv. r.* cervical ribs; *f. trs.* probe passed into foramen triosseum; *fur.* furcula; *gl. cv.* glenoid cavity; *il.* ilium; *is.* ischium; *is. for.* ischiatic foramen; *obt. n.* obturator notch; *pu.* pubis; *pyg.st.* pygostyle; *scp.* scapula; *s. scr.* syn-sacrum; *st.* sternum; *st. r.* sternal ribs; *th. v. 1*, first, and *th. v. 5*, last thoracic vertebra; *unc.* uncinates; *vr. r.* vertebral ribs.

The centra articulate with one another by synovial capsules each traversed by a vertical plate of cartilage, the *meniscus,* with a central perforation through which a *suspensory ligament* passes from one centrum to the other.

The first two vertebræ, the atlas and axis, resemble those of the Lizard, but have the various elements of which they are composed completely fused. The small size of the ring-like atlas is noticeable.

Between the last cervical vertebræ and the pelvic region come four thoracic vertebræ (Fig. 968), the first three united into a single mass, the fourth free. The anterior thoracic as well as the posterior cervical vertebræ have the centrum produced below into a compressed plate, the *hypapophysis,* for the origin of the flexor muscles

of the neck. They all bear ribs, each consisting of a vertebral (*vr.r.*) and a sternal (*st.r.*) portion, and articulating with the vertebra by a double head. The sternal, like the vertebral rib, is formed of true bone, not of calcified cartilage as in Reptiles, and articulates with the vertebral rib by a synovial joint. Springing from the posterior edge of the vertebral rib is an *uncinate* (*unc.*), resembling that of Hatteria and the Crocodile, but formed of bone and ankylosed with the rib.

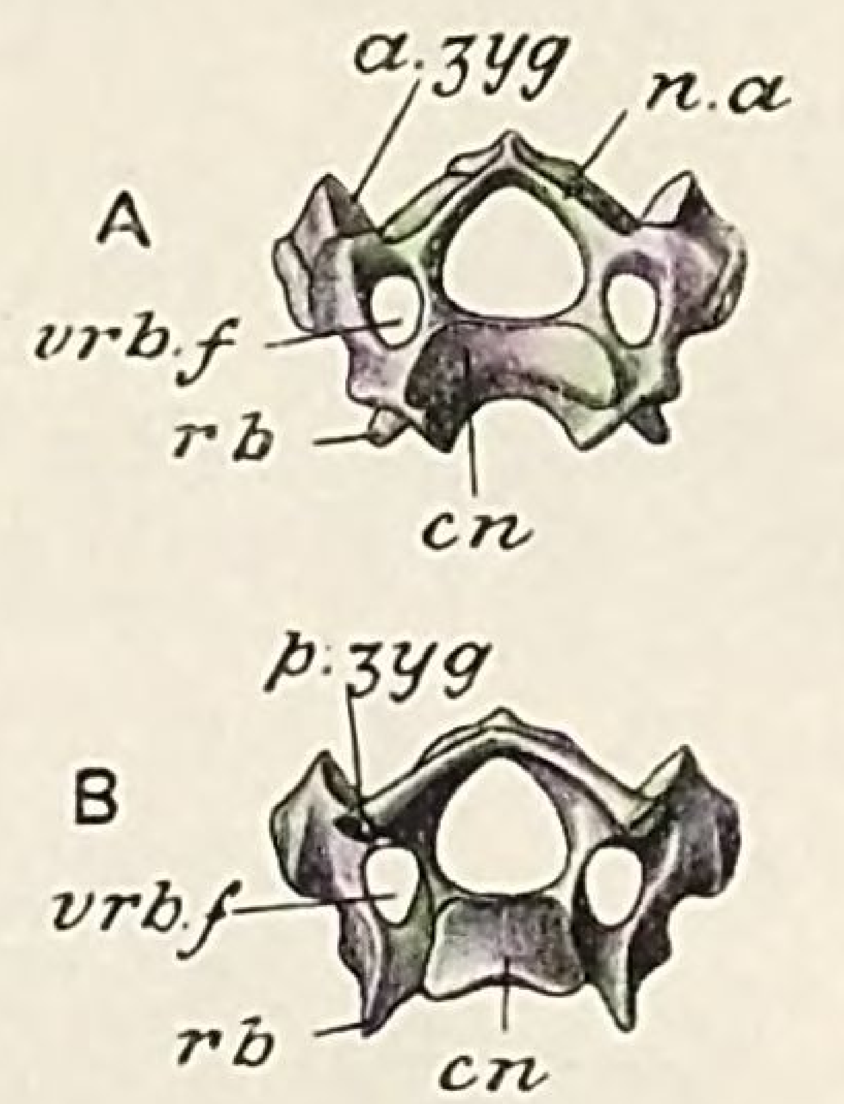


FIG. 969.—**Columba livia.** Cervical vertebra. A, anterior; B, posterior face. *a. zyg.* anterior zygapophysis; *cn.* centrum; *n. a.* neural arch; *p. zyg.* posterior zygapophysis; *r.* rib; *vrb. f.* vertebrarterial foramen.

Following upon the fourth thoracic are about twelve vertebræ all fused into a single mass (Fig. 968, *s.scr.*), and giving attachment laterally to the immense pelvic girdle. The whole of this group of vertebræ has, therefore, the function of a sacrum, differing from that of a Reptile in the large number of vertebræ composing it. The first of them bears a pair of free ribs, and is, therefore, the fifth or last thoracic (*th.v. 5*). The next five or six have no free ribs, and may be looked upon as lumbar (Fig. 970, *l. 1—s. 3*): their tranverse processes arise high up on the neural arch and the ligament uniting them is ossified so that the lumbar region presents dorsally a continuous plate of bone. Next come two sacral vertebræ (*c.1*) homologous with those of the Lizard: besides transverse processes springing from the neural arch, one or both of them bears a second or ventral outgrowth (*c.r.*) springing from each side of the centrum and abutting against the ilium just internal to the acetabulum. These distinctive processes are ossified independently and represent sacral ribs. The remaining five vertebræ of the pelvic region are caudal. Thus the mass of vertebræ supporting the pelvic girdle in the Pigeon is a compound sacrum, or *syn-sacrum*, formed by the fusion of the posterior thoracic, all the lumbar and sacral, and the anterior caudal vertebræ.

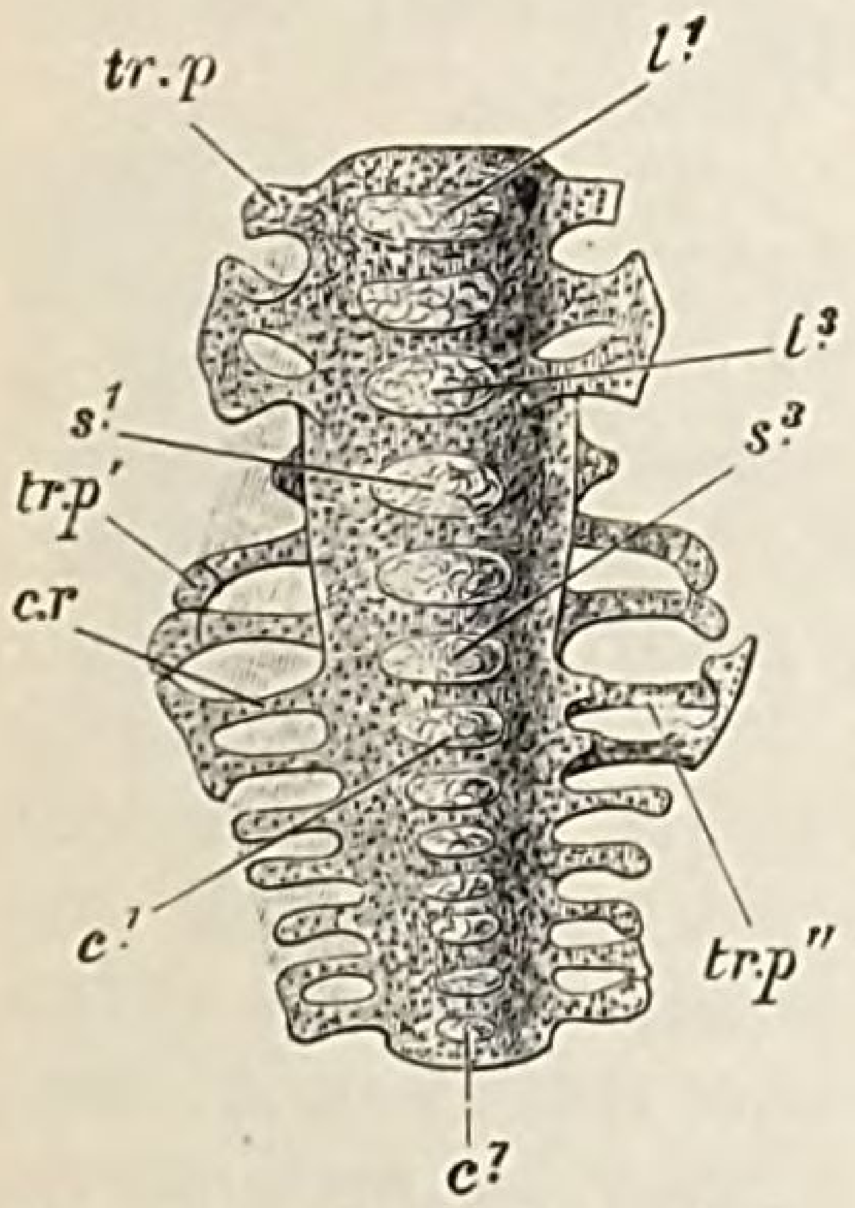


FIG. 970.—**Columba livia.** Sacrum of a nestling (about fourteen days old), ventral aspect. c^1. centrum of first sacral vertebra; c^1. centrum of fifth caudal; *c. r.* first sacral rib; l^1. centrum of first lumbar; l^3. of third lumbar; s^1, of fourth lumbar; s^3, of sixth lumbar; *tr. p.* transverse process of first lumbar; *tr. p'.* of fifth lumbar; *tr. p''.* of first sacral. (From Parker's *Zootomy*.)

The syn-sacrum is followed by six free caudals, and the vertebral column ends posteriorly in an upturned, compressed

bone, the *pygostyle* or ploughshare-bone (Fig. 968, *pyg.st.*), formed by the fusion of four or more of the hindmost caudal vertebræ.

Thus the composition of the vertebral column of the Pigeon may be expressed in a *vertebral formula* as follows:—

		Syn-sacrum.			Pyg.
Cerv. 14.	Thor. 1 + 3 +	1. Lumb. 6. Sacr. 2. Caud. 5	+ 6 +	4	= 42.

The *sternum* (Fig. 968, *st.*) is one of the most characteristic parts of the Bird's skeleton. It is a broad plate of bone produced ventrally, in the sagittal plane, into a deep keel or *carina sterni* (*car.*), formed, in the young Bird, from a separate centre of ossification. The posterior border of the sternum presents two pairs of notches, covered, in the recent state, by ligament; its anterior edge bears a pair of deep grooves for the articulation of the coracoids.

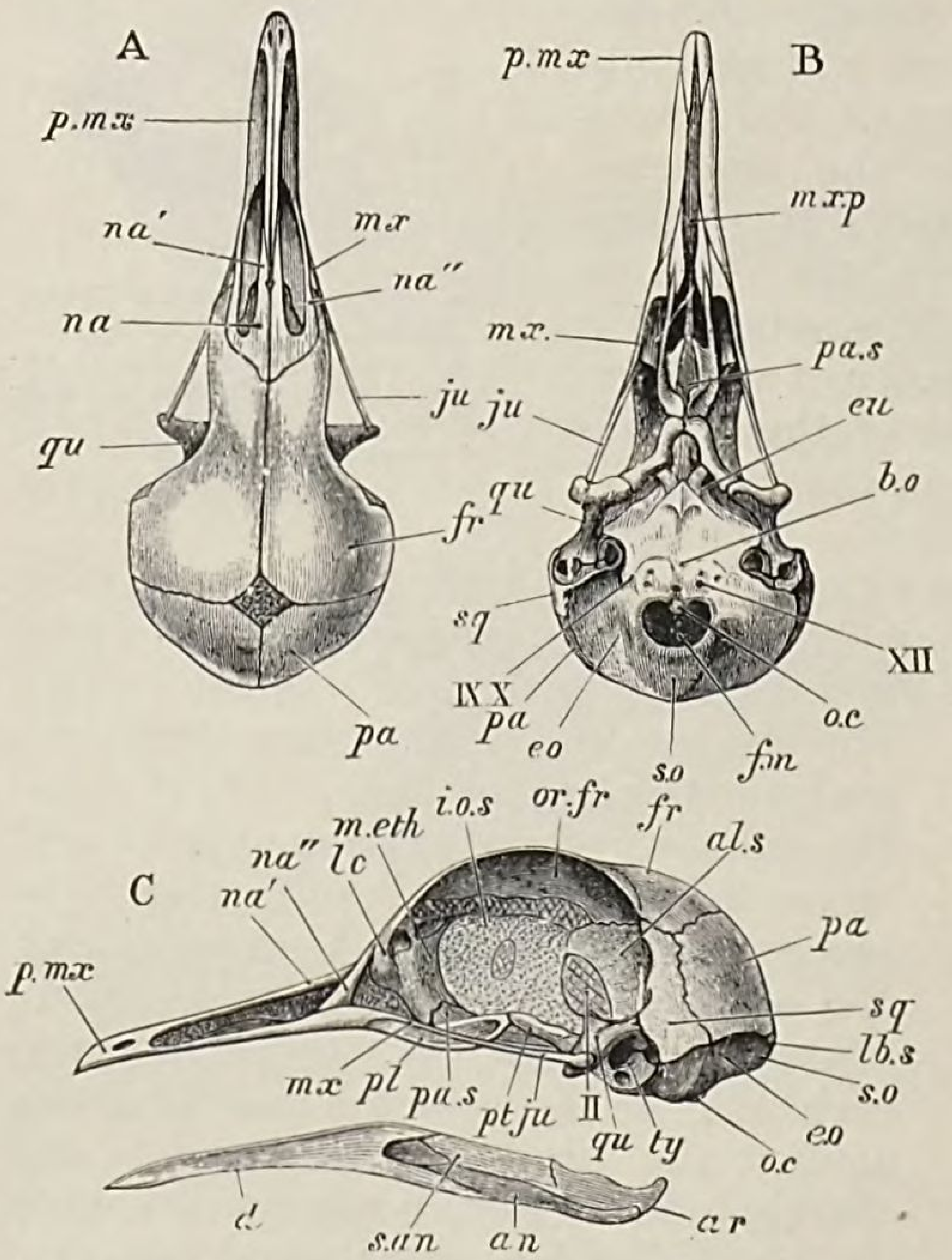


FIG. 971.—**Columba livia.** Skull of young specimen. A dorsal; B, ventral; C, left side, *al.s.* alisphenoid; *an.* angular; *ar.* articular; *b. o.* basi-occipital; *d.* dentary; *e. o.* ex-occipital; *eu.* aperture of Eustachian tube; *f. m.* foramen magnum; *fr.* frontal; *i. o. s.* inter-orbital septum; *ju.* jugal; *lc.* lacrymal; *lb.s.* lambdoidal suture; *m.eth.* mesethmoid; *mx.* maxilla; *mx. p.* maxillo-palatine process; *na. na'. na''.* nasal; *o. c.* occipital condyle; *or. fr.* orbital plate of frontal; *pa.* parietal; *pa.s.* parasphenoid (rostrum); *pl.* palatine; *p. mx.* pre-maxilla; *pt.* pterygoid; *qu.* quadrate; *s. an.* supra-angular; *s. o.* supra-occipital; *sq.* squamosal; *ty.* tympanic cavity; II—XII, foramina for cerebral nerves. (From Parker's *Zootomy.*)

The *skull* (Fig. 971) is distinguished at once by its rounded brain-case, immense orbits, and long, pointed beak. The foramen magnum (*f. m.*) looks downwards as well as backwards, so as to be visible in a ventral view, and on its anterior margin is a single, small, rounded occipital condyle (*o.c.*). Most of the bones, both of the cranial and facial regions, are firmly ankylosed in the adult, and can be made out only in the young Bird.

The occipitals, parietals, frontals, and alisphenoids have the usual

relations to the brain-case, the basi-occipital (*b.o.*) as in the Lizard, bearing the occipital condyle. The basi-sphenoid (Fig. 972, B. SPH) is a large bone forming the greater part of the basis cranii, and continued forwards, as in the Lizard, by a slender *rostrum* (Fig. 971, *pa.s.*, Fig. 972, *RST.*), which represents the anterior portion of the para-sphenoid. On the ventral aspect of the basi-sphenoid paired membrane bones, the *basi-temporals* (Fig. 972, *B. TMP*) are developed, and become firmly ankylosed to it in the adult: they probably represent the posterior portion of the para-sphenoid. The tympanic cavity is bounded by the squamosal (Fig. 971, *sq.*), which is firmly united to the other cranial bones. The main part

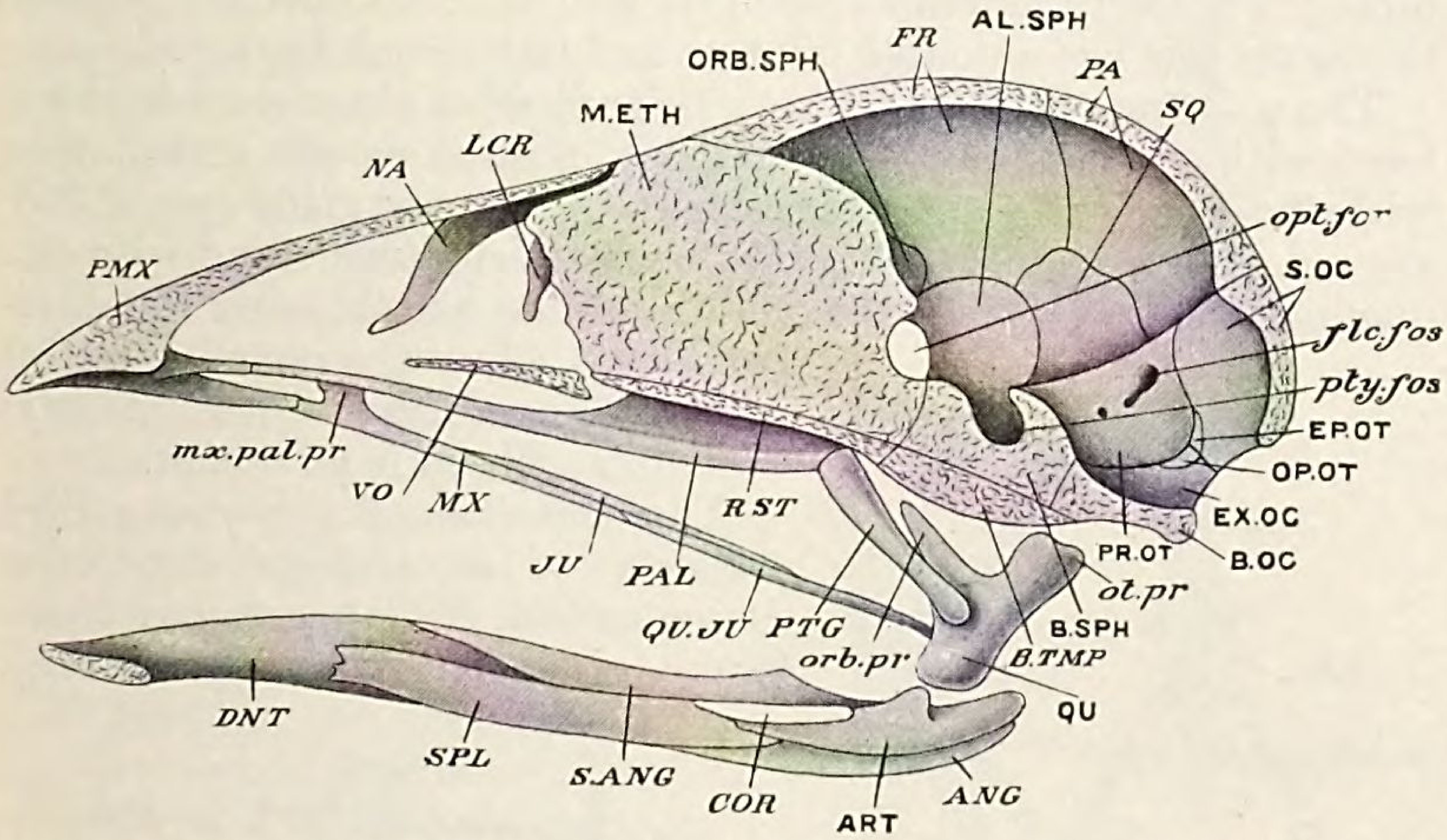


FIG. 972.—Sagittal section of a **Bird's** skull (diagrammatic). *Cartilage bones*—**AL.SFH.** alisphenoid; **ART.** articular; **B.OC.** basi-occipital; **EP.OT.** epiotic; **EX.OC.** ex-occipital; **M.ETH.** mesethmoid; **OP.OT.** opisthotic; **ORB.SPH.** orbito-sphenoid; **PR.OT.** pro-otic; **QU.** quadrate; **S. OC.** supra-occipital. *Membrane bones*—*ANG.* angular; *B. TMP.* basi-temporal; *COR.* coronary; *DNT.* dentary; *FR.* frontal; *JU.* jugal; *LCR.* lacrymal; *MX.* maxilla; *NA.* nasal; *PA.* palatine; *PMX.* pre-maxilla; *PTG.* pterygoid; *QU. JU.* quadrato-jugal; *RST.* rostrum; *S. ANG.* supra-angular; *SPL.* splenial; *SQ.* squamosal; *VO.* vomer; *flc. fos.* floccular fossa; *mx. pal. pr.* maxillo-palatine process; *opt. for.* optic foramen; *orb. pr.* orbital process; *ot. pr.* otic process; *pty. fos.* pituitary fossa.

of the auditory capsule is ossified by a large pro-otic (Fig. 972, PR. OT): the small opisthotic of the embryo early unites with the exoccipital, the epiotic with the supra-occipital. The presphenoid and mesethmoid together form the *interorbital septum* (Fig. 971, *i.o.s.*), a vertical partition, partly bony, partly cartilaginous, which separates the orbits from one another. It is very characteristic of the Bird's skull that the immense size of the eyes has produced a compression of this region of the skull. The ectoethmoids or turbinals are comparatively poorly developed, in correspondence with the small size of the olfactory organs. There are large lacrymals (Fig. 971, *lc.*, Fig. 972, *LCR.*) and the nasals (*na*, *na′*, *na″*; *NA*) are forked bones each furnishing both an inner and an outer boundary to the corresponding nostril.

The premaxillæ (*p.mx.*, *PMX.*) are united into a large triradiate bone which forms practically the whole of the upper beak. The maxillæ (*mx.*, *MX.*), on the other hand, are small, and have their anterior ends produced inwards into spongy *maxillo-palatine processes* (Fig. 971, *mx.p.*, Fig. 972, *mx.pal.pr.*). The slender posterior end of the maxilla is continued backwards by an equally slender jugal (*ju.*, *JU.*) and quadrato-jugal (*QU. JU.*), to the quadrate. The latter (*qu.*, QU.) is a stout three-rayed bone articulating by two facets on its *otic process* (*ot. pr.*) with the roof of the tympanic cavity, sending off an *orbital process* (*orb. pr.*) from its anterior margin, and presenting below a *condyle* for articulation with the mandible; it is freely moveable upon its tympanic articulation, so that the lower jaw has a double joint as in Lizards and Snakes.

The palatines (*pl.*, *PAL.*) have their slender anterior ends ankylosed with the maxilla, their scroll-like posterior ends articulating with the pterygoids and the rostrum. The pterygoids (*pt.*, *PTG*). are rod-shaped and set obliquely: each articulates behind with the quadrate, and, at about the middle of its length, with the *basi-ptery-goid process*, a small facetted projection of the base of the rostrum. There is no vomer.

The *mandible* of the young Bird consists of a cartilage bone, the articular (*ar.*, ART.), and four membrane bones, the angular (*an.*, *ANG.*),

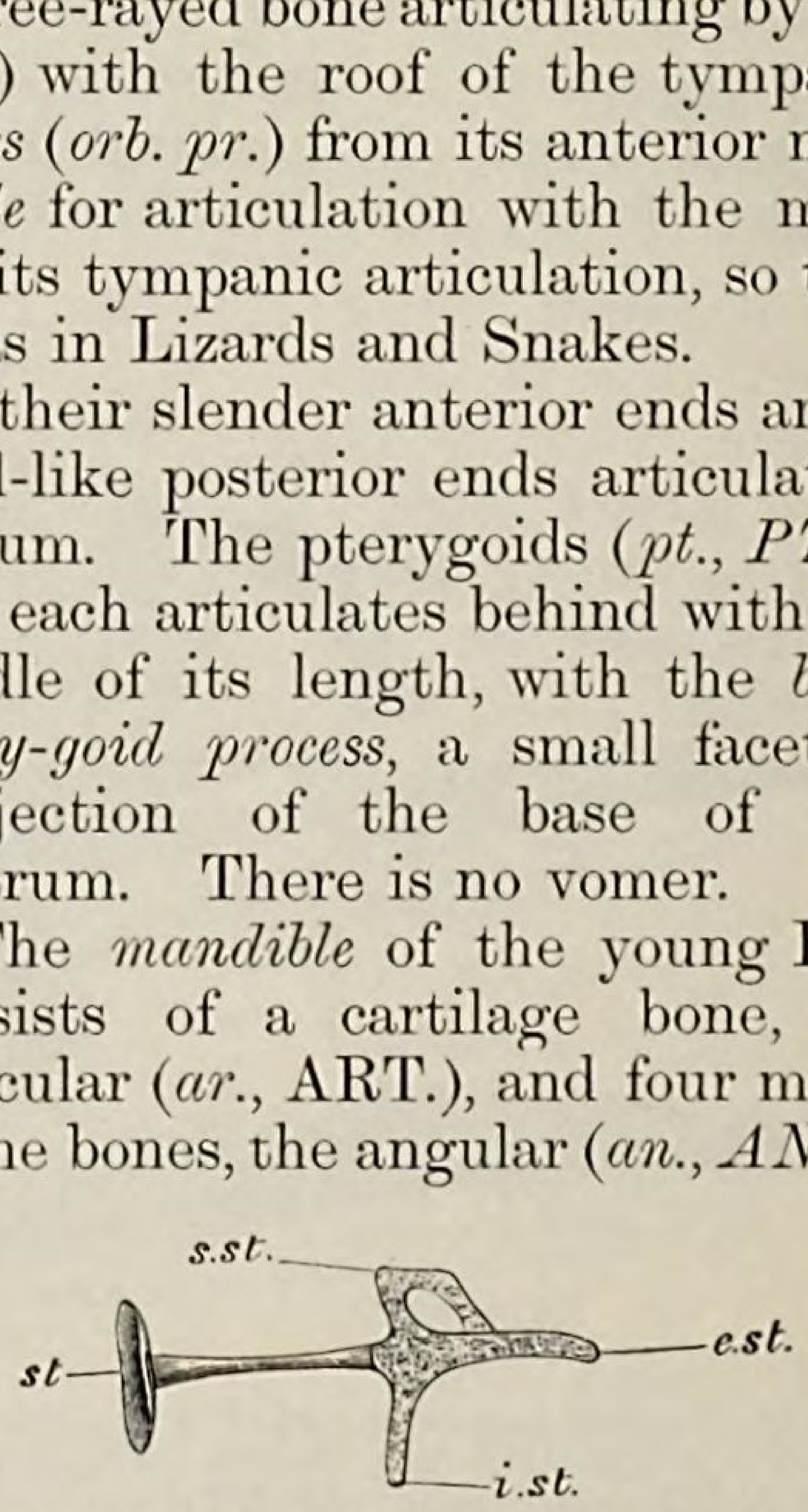


FIG. 974.—**Columba livia.** The columella auris (magnified). The cartilaginous parts are dotted. *e. st.* extra-stapedial; *i. st.* infra-stapedial; *s. st.* supra-stapedial; *st.* stapes. (From Parker's *Zootomy*.)

supra-angular (*s.an.*, *S.ANG.*), dentary (*d.*, *DNT.*), and splenial (*SPL.*), all having the same general relations as in the Lizard. The *hyoid apparatus* (Fig. 973), is of characteristic form, having an arrow-shaped body (*b. hy.*) with a short pair of anterior cornua (*c. hy.*) derived from the hyoid arch, and a long pair of posterior cornua (*c.br.*, *ep.br.*) from the first branchial. The *columella* (Fig. 974) is a rod-shaped bone ankylosed to the stapes, and bearing at its outer end a three-rayed cartilage or *extra-columella* (*e.st.*, *i.st.*, *s.st.*) fixed to the tympanic membrane.

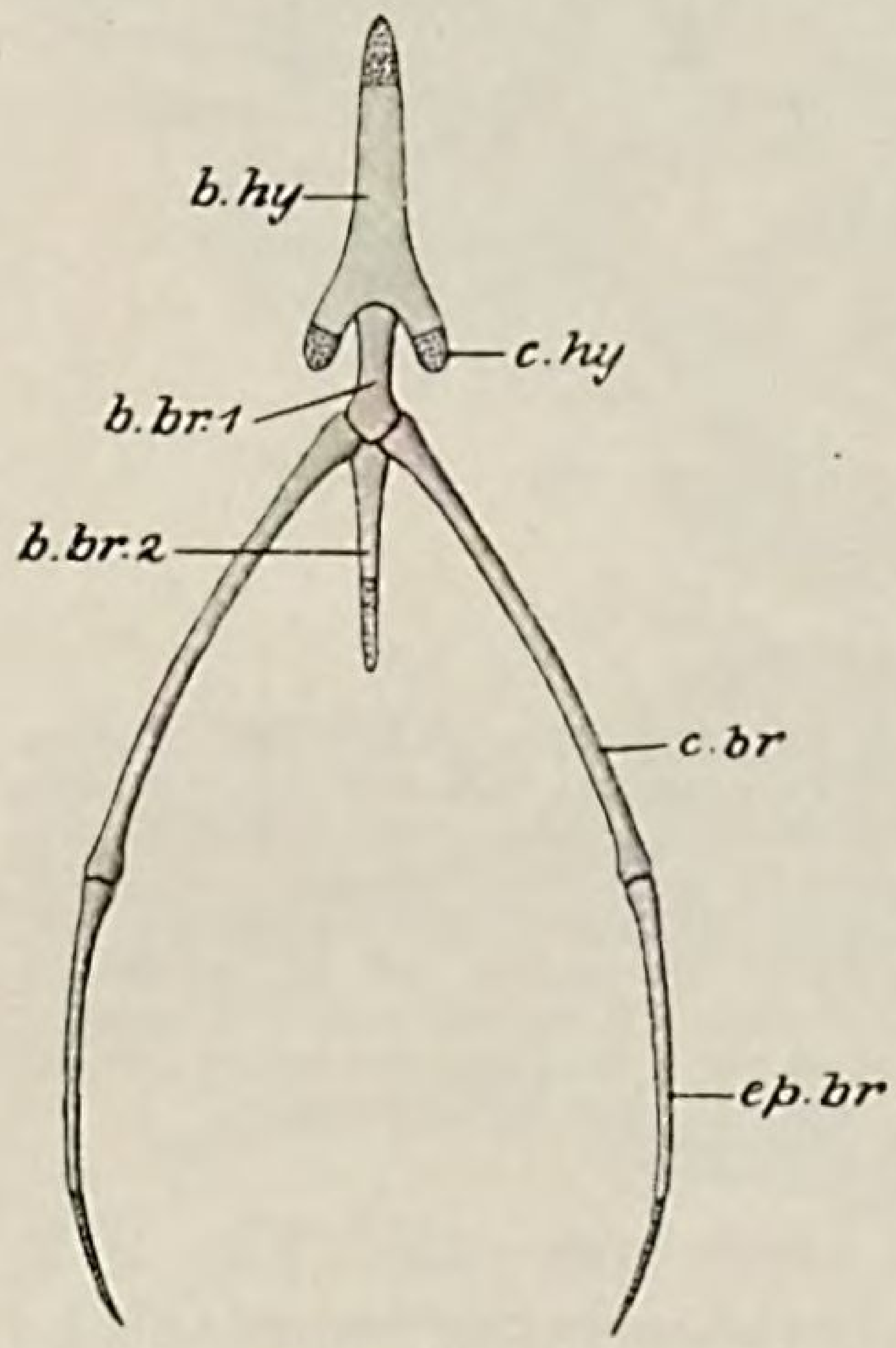


FIG. 973.—**Columba livia.** Hyoid apparatus. The cartilaginous parts are dotted. *b. br.1*, basi-branchials; *b.hy.* basi-hyal; *c.br.* cerato-branchial; *c. hy.* hyoid cornu; *ep. br.* epi-branchial.

The *shoulder-girdle* (Fig. 968) is quite unlike that of other

Craniates. There is a pair of stout, pillar-like *coracoids* (*cor.*) articulating with deep facets on the anterior border of the sternum and directed upwards, forwards, and outwards. The dorsal end of each is produced into an *acrocoracoid process* (*acr. cor*), and below this, to the posterior aspect of the bone, is attached by ligament a sabre-shaped *scapula* (*scp.*) which extends backwards over the ribs, and includes, with the coracoid, an acute angle, the *coraco-scapular angle.* The glenoid cavity (*gl. cv.*) is formed in equal proportion by the two bones; internal to it the scapula is produced into an *acromion process.* In front of the coracoids is a slender V-shaped bone, the *furcula* (*fur.*) or "merrythought," the apex of which nearly reaches the sternum, while each of its extremities is attached by ligament to the acromion and acro-coracoid processes of the corresponding side, in such a way that a large aperture, the *foramen triosseum* (*f. trs.*) is left between the three bones of the shoulder-girdle. The furcula is a membrane bone and represents fused clavicles and interclavicle.

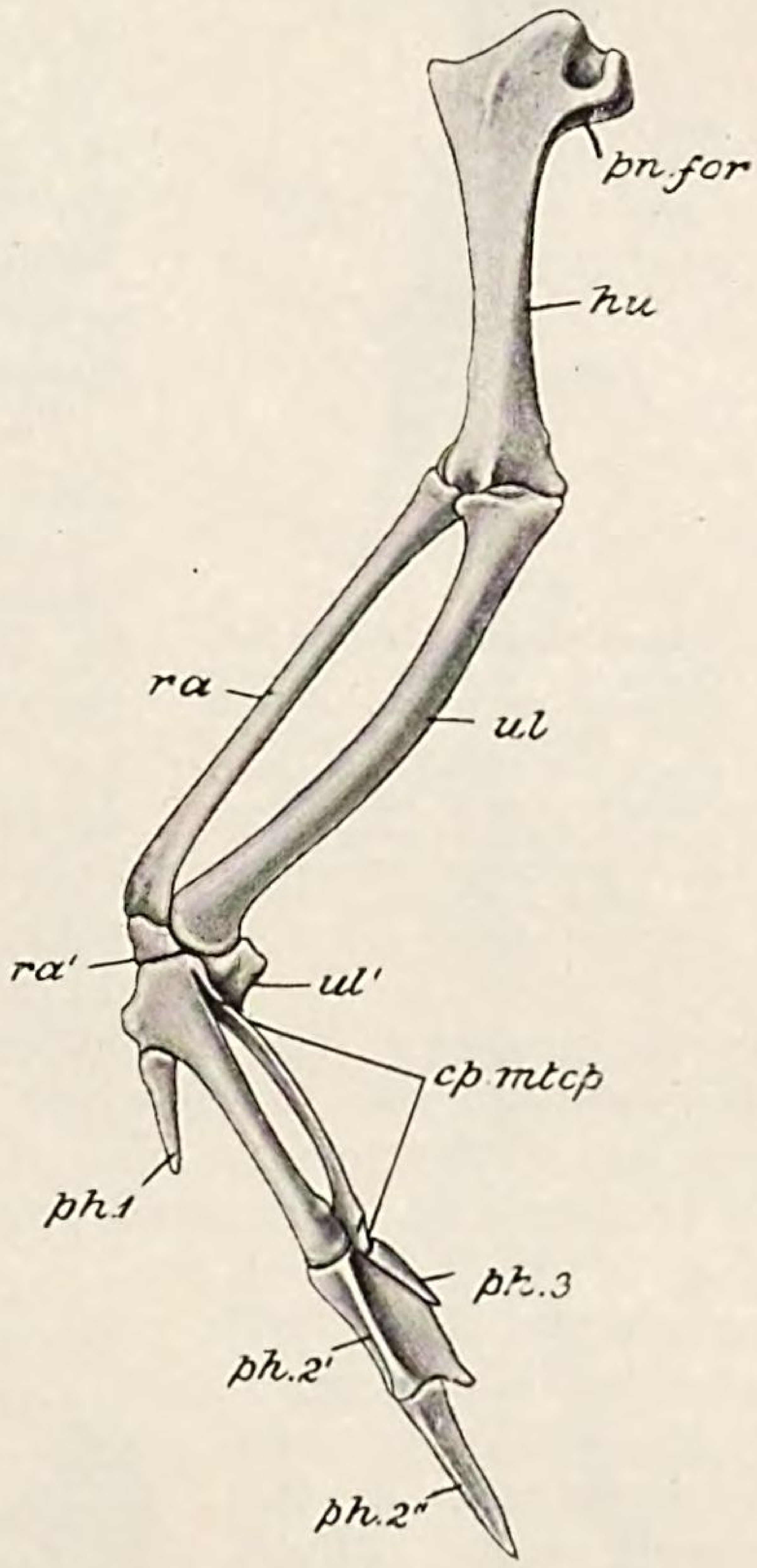


FIG. 975.—**Columba livia.** Skeleton of the left wing. *cp. mtcp.* carpo-metacarpus; *hu.* humerus; ph. *1*, phalanx of first digit; *ph.2'*, *ph.2''*, phalanges of second digit; *ph.3*, phalanx of third digit; *pn. for.* pneumatic foramen. *RA.* radius; *ra.* radiale; *Ul* ulna; *ul.* ulnare.

Equally characteristic is the skeleton of the fore-limb. The *humerus* (Fig. 975, *hu.*) is a large, strong bone, with a greatly expanded head and a prominent ridge for the insertion of the pectoral muscle. In it, as in all the other long bones, the extremities as well as the shaft are formed of true bone. The *radius* (*ra.*) is slender and nearly straight, the *ulna* stouter and gently curved. There are two large free carpals, a *radiale* (*ra.'*) and an *ulnare* (*ul.'*), and articulating with these is a bone called the *carpo-metacarpus* (*cp.mtcp.*) consisting of two rods, that on the preaxial side strong and nearly straight, that on the postaxial side slender and curved, fused with one another at both their proximal and distal ends; the proximal end is produced,

pre-axially, into an outstanding step-like process. The study of development shows that this bone is formed by the union of the distal carpals with three metacarpals (Fig. 976), the second and third of which are the two rod-like portions of the bone, the first the step-like projection. Articulating with the first metacarpal is a single pointed phalanx (*ph. 1*); the second metacarpal bears two phalanges, the proximal one (*ph. 2′*) produced postaxially into a flange, the distal one (*ph. 2″*) pointed; the third metacarpal bears a single pointed phalanx (*ph. 3*).

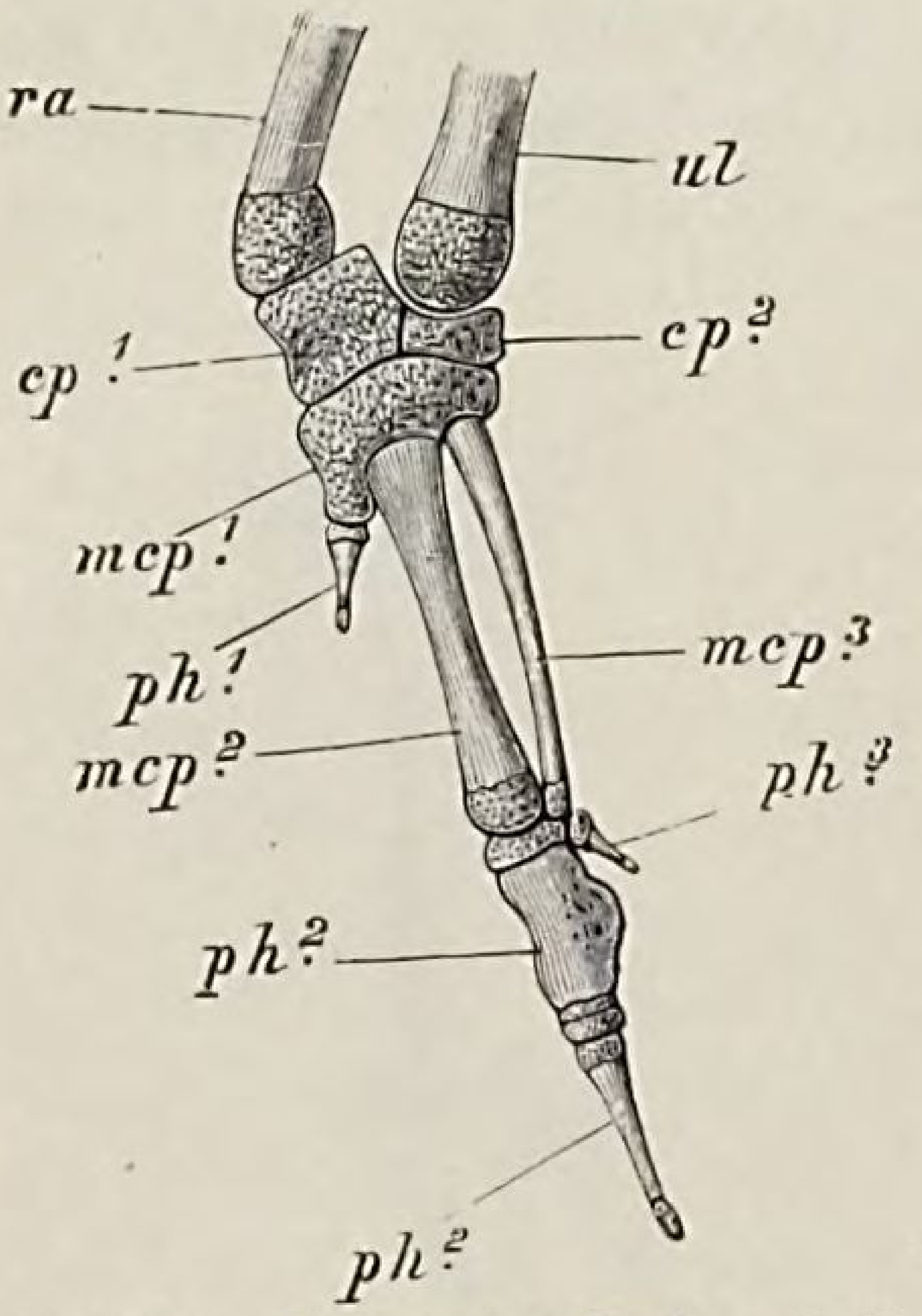


FIG. 976.—**Columba livia.** Left manus of a nestling. The cartilaginous parts are dotted. *cp. 1*, radiale; *cp. 2*, ulnare; *mcp. 1, 2, 3*, metacarpals; *ph. 1*, phalanx of first digit; *ph. 2*, *ph. 2′*, phalanges of second digit; *ph. 3*, phalanx of third digit; *ra.* radius; *ul.* ulna. (From Parker's *Zootomy*.)

The *pelvic girdle* (Fig. 968) resembles that of no other vertebrate with the exception of some Dinosaurs. The *ilium* (*il.*) is an immense bone, attached by fibrous union with the whole of the syn-sacrum and becoming ankylosed with it in the adult. It is divisible into *pre-acetabular* and *post-acetabular* portions of approximately equal size. As usual it furnishes the dorsal portion of the acetabulum, and on the posterior edge of that cavity is produced into a process, the *antitrochanter* (*a.tr.*) which works against the trochanter, a process of the femur. The ventral portion of the acetabulum is furnished in about equal proportions by the pubis and ischium (Fig. 977): it is not completely closed by bone, but is perforated by an aperture covered by membrane in the recent state. Both pubis and ischium are directed sharply backwards from their dorsal or acetabular ends. The *ischium* (*is.*) is a broad bone, ankylosed posteriorly with the ilium, and separated from it in front by an *ischiatic foramen* (*is.for.*). The *pubis* (*pu.*) is a slender, curved rod, parallel with the ventral edge of the ischium, and separated from it by an *obturator notch* (*obt.n.*).

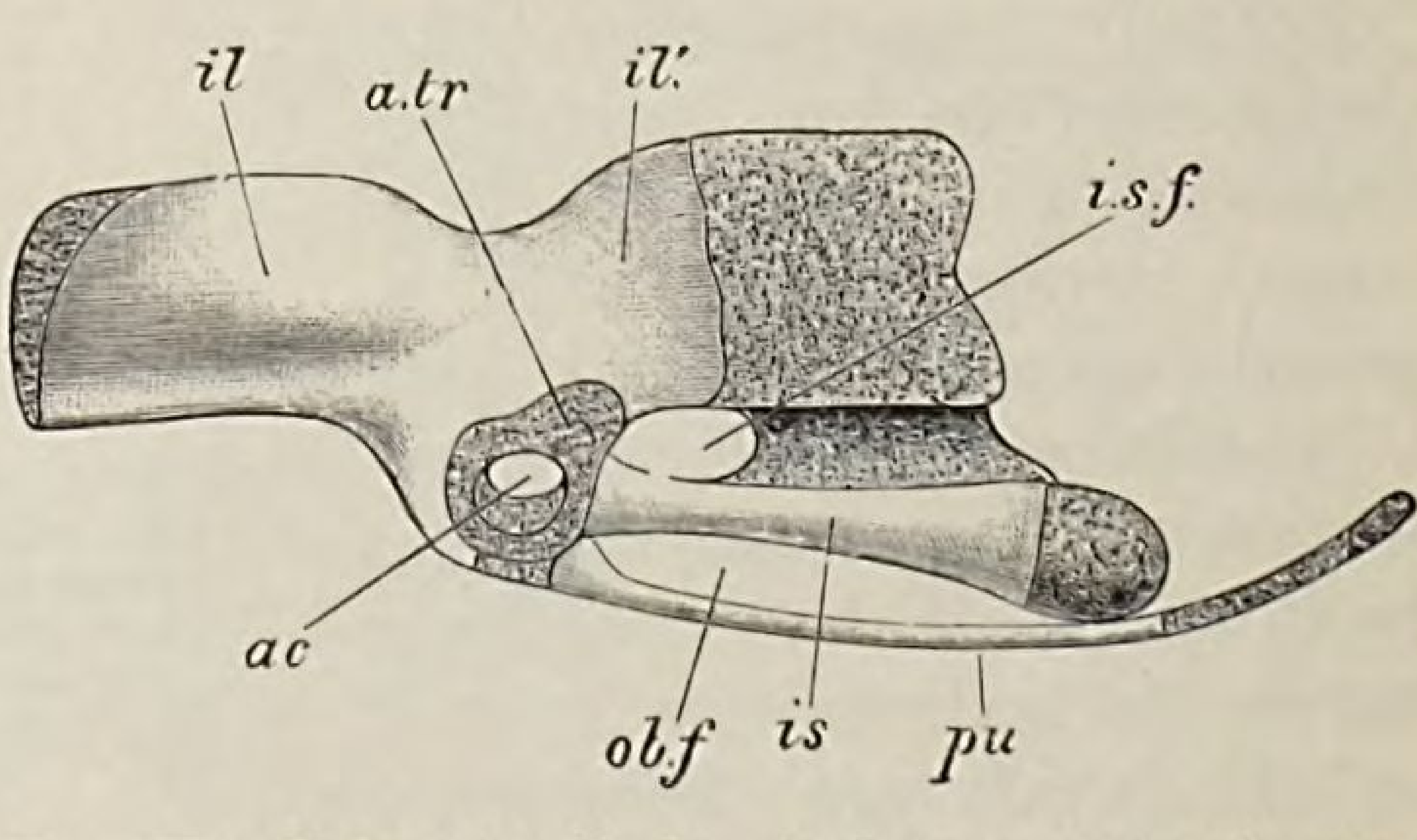


FIG. 977.—**Columba livia.** Left innominate of a nestling. The cartilage is dotted. *ac.* acetabulum; *a. tr.* anti-trochanter; *il.* pre-acetabular; and *il′.* post-acetabular portion of ilium; *is.* ischium; *i. s. f.* ischiatic foramen; *ob. f.* obturator notch; *pu.* pubis. (From Parker's *Zootomy*.)

Neither ischium nor pubis unites ventrally with its fellow to form a symphysis.

In the hind-limb the *femur* (Fig. 978, *fe.*) is a comparatively short bone. Its proximal extremity bears a prominent *trochanter* (*tr.*) and a rounded *head* (*hd.*), the axis of which is at right angles to the shaft of the bone, so that the femur, and indeed the whole limb, lies in a plane parallel with the sagittal plane of the trunk, and is not directed outwards as in Reptiles. Its distal end is produced into pulley-like *condyles*. There is a small sesamoid bone, the *patella* (*pat.*), developed on the extensor side of the knee-joint. Articulating with the femur is a very long bone, the *tibio-tarsus* (*ti.ts.*) produced on the anterior face of its proximal end into a large *cnemial process* (*cn.pr.*) for the insertion of the extensor muscle of the thigh. Its proximal articular surface is slightly hollowed for the condyle of the femur, its distal end is pulley-like, not concave like the corresponding extremity of the tibia of other Amniota. The study of development shows that the pulley-like distal end of the bone (Fig. 979, *tl.1*) consists of the proximal tarsals—astragalus and calcaneum—which at an early period unite with the tibia and give rise to the compound shank-bone of the adult. The *fibula* (*fi.*) is very small, much shorter than the tibia, and tapers to a point at its distal end.

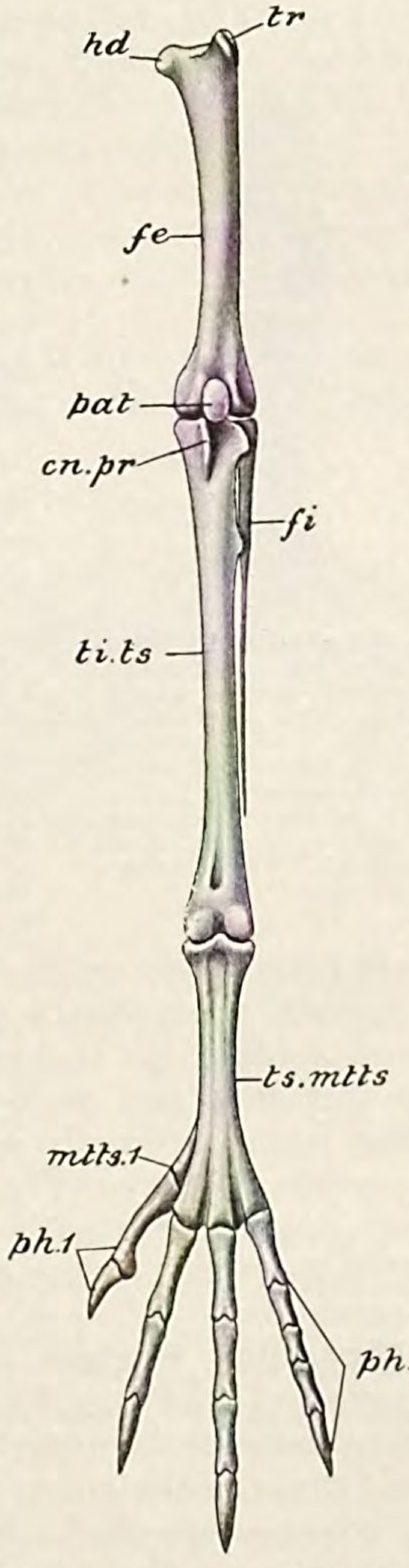


FIG. 978.—**Columba livia.** Bones of the left hind-limb. *cn. pr.* cnemial process; *fe.* femur; *fi.* fibula; *hd.* head; *mtts. 1,* first metatarsal; *pat.* patella; *ph. 1,* phalanx of first digit; *ph.4,* phalanx of fourth digit; *ti. ts.* tibio-tarsus; *ts. mtts.* tarso-metatarsus; *tr.* trochanter.

Following the tibio-tarsus is an elongated bone, the *tarso-metatarsus* (*ts. mtts.*), presenting at its proximal end a concave surface for the tibio-tarsus, and at its distal end three distinct pulleys for the articulation of the three forwardly-directed toes. In the young Bird the proximal end of this bone is a separate cartilage (Fig. 979, *tl.2*), representing the distal tarsals, and followed by three distinct metacarpals,

belonging respectively to the second, third, and fourth digits. Thus the ankle-joint of the bird is a *meso-tarsal* joint, occurring, as in the Lizard, between the proximal and distal tarsals, and not, as in other Amniota, between the tibia and the proximal tarsals. To the inner or preaxial side of the tarso-metatarsus, near its distal end, is attached by fibrous tissue a small irregular bone, the first metatarsal (*mtts. 1*). The digits have the same number of phalanges as in the Lizard, the backwardly-directed hallux two, the second or inner toe three, the third or middle toe four, and the fourth or outer toe five. In all four digits the distal or ungual phalanx is pointed and curved, and serves for the support of the horny claw.

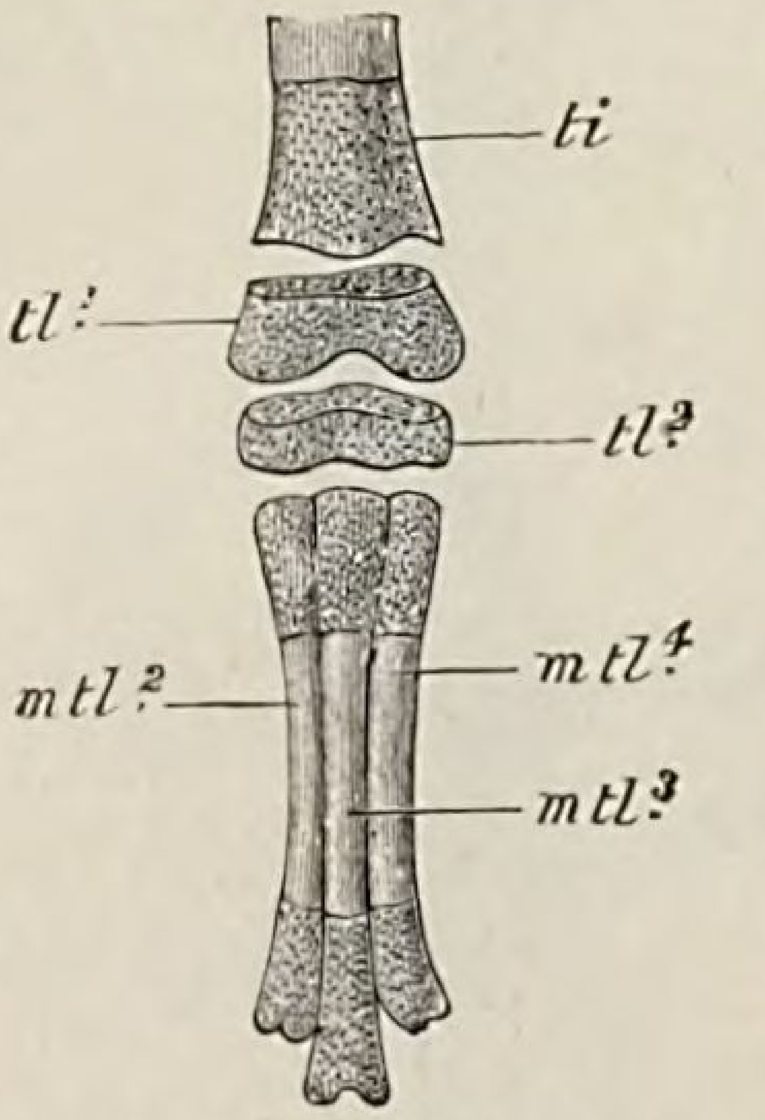


FIG. 979.—**Columba livia.** Part of left foot of an unhatched embryo (magnified). The cartilage is dotted. *mtl. 2*, second; *mtl. 3*, third; and *mtl. 4*, fourth metatarsal; *ti.* tibia; *tl. 1*, proximal tarsal cartilage; *tl. 2*, distal tarsal cartilage. (From Parker's *Zootomy*.)

It will be observed that every part of the Bird's skeleton presents characteristic and indeed unique features. The vertebral column, the skull, the sternum, the ribs, the limb-girdles, and the limbs themselves are all so highly specialised that there is hardly a bone, except the phalanges of the toes and the free caudal vertebræ, which could possibly be assigned to any other vertebrate class.

A further peculiarity is the fact that the larger proportion of the bones contain no marrow, but are filled during life with air, and are therefore said to be *pneumatic*. The cavities of the various bones open externally in the dried skeleton by apertures called *pneumatic foramina* (Fig. 975, *pn. fr.*), by which, in the entire bird, they communicate with the air-sacs (*vide infra*). In the Pigeon the bones of the fore-arm and hand, and of the leg, are non-pneumatic.

Muscular System.—As might naturally be expected the muscles of the fore-limb are greatly modified. The powerful downstroke of the wing by which the bird rises into, and propels itself through the air, is performed by the *pectoralis* (Fig. 980, *pct.*), an immense muscle having about one-fifth the total weight of the body; it arises from the whole of the keel of the sternum (*car. st.*), from the posterior part of the body of that bone (*cp. st.*), and from the clavicle (*cl.*), filling nearly the whole of the wedge-shaped space between the body and the keel of the sternum and forming what is commonly called the "breast" of the Bird. Its fibres converge to their insertion (*pct.''*) into the ventral aspect of the humerus (*hu.*, *hu'.*) which it depresses. The elevation of the wing is performed, not, as might be expected, by a dorsally placed muscle, but by the *subclavius* (*sb. clv.*), arising from the anterior part of the

body of the sternum, dorsal to the pectoralis, and sending its tendon (*sb. clv.'*) through the foramen triosseum to be inserted into the dorsal aspect of the humerus. In virtue of this arrangement, the end of the foramen acting like a pulley, the direction of action of the muscle is changed, the backward pull of the tendon raising the humerus. There are three *tensores patagii* (*tns. lg.*, *tns. br.*, *tns. acc.*), the action of which is to keep the pre-patagium tensely stretched when the wing is extended. A similar muscle (*tns. m. p*) acts upon the post-patagium. The muscles of the digits are naturally much reduced.

The muscles of the neck and tail are well developed, those of the back are practically atrophied, in correspondence with the im-

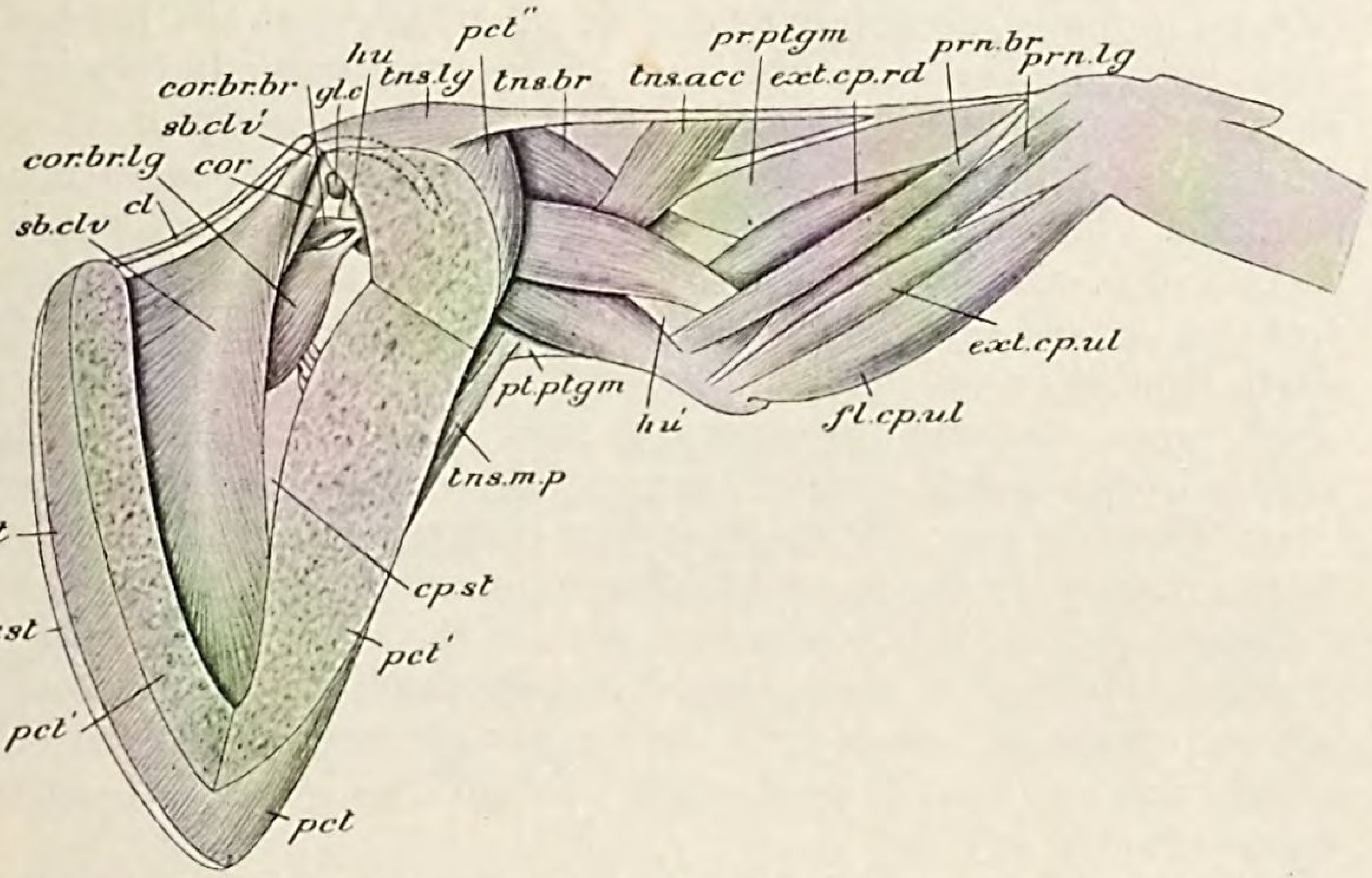


FIG. 980.—**Columba livia.** The principal muscles of the left wing; the greater part of the pectoralis (*pct.*) is removed. *car. st.* carina sterni; *cl.* furcula; *cor.* coracoid; *cor. br. br.* coraco-brachialis brevis; *cor. br. lg.* coraco-brachialis longus; *cp. st.* corpus sterni; *ext. cp. rd.* extensor carpi radialis; *ext. cp. ul.* extensor carpi ulnaris; *fl. cp. ul.* flexor carpi ulnaris; *gl. c.* glenoid cavity; *hu.* head of humerus; *hu'.* its distal end; *pct.* pectoralis; *pct'.* its cut edge; *pct''.* its insertion; *prn. br.* pronator brevis; *prn. lg.* pronator longus; *pr. ptgm.* pre-patagium; *pt. ptgm.* post-patagium; *sb. clv.* sub-clavius; *sb. clv'.* its tendon of insertion passing through the foramen triosseum, and dotted as it goes to the humerus; *tns. acc.* tensor accessorius; *tns. br.* tensor brevis; *tns. lg.* tensor longus; *tns. m. p.* tensor membranæ posterioris alæ.

mobility of that region. In the leg certain of the muscles are modified to form the *perching mechanism.* The toes are flexed by two sets of tendons, deep and superficial. The deep tendons of the three forwardly directed digits are formed by the trifurcation of the tendon of a single muscle, the *peronæus medius*, that of the hallux is derived from a separate muscle, the *flexor perforans*, which is joined by a slip from the peronæus medius. Thus a pull upon one tendon flexes all the toes. When the leg is bent, as the bird settles to roost, the flexion of the tarso-metatarsus on the shank puts the flexor tendons on the stretch as

they pass over the mesotarsal joint, and by the pull thus exerted the toes are automatically bent round the perch by the simple action of flexing the leg. They are kept in this position while the Bird is asleep by the mere weight of the body. The action is assisted by a small but characteristic muscle, the *ambiens*, which arises from the pubis, passes along the inner surface of the thigh, and is continued into a long tendon which comes round to the outer side of the knee, enclosed in a special sheath, and, continuing down the leg, joins the superficial flexors of the digits.

Digestive Organs.—The *mouth* (Fig. 981) is bounded above and below by the horny beaks, and there is no trace of teeth. The *tongue* (*tng.*) is large and pointed at the tip. The pharynx leads into a wide and distensible *gullet* (*gul.*) which soon dilates into an immense reservoir or *crop* (*crp.*) situated at the base of the neck, between the skin and the muscles, and immediately in front of the sternum. In this cavity the food, consisting of grain, undergoes a process of maceration before being passed into the stomach. From the crop the gullet is continued backwards into the *stomach*, which consists of two parts, the *proventriculus* (*prvn.*) and the *gizzard* (*giz.*). The proventriculus appears externally like a slight dilatation of the gullet; but its mucous membrane is very thick, and contains numerous gastric glands so large as to be visible to the naked eye. The gizzard has the shape of a biconvex lens: its walls are very thick and its lumen small. The thickening is due mainly to the immense development of the muscles which radiate from two tendons one on each of the convex surfaces. The epithelial lining of the gizzard is very thick and horny, and of a yellow or green colour: its cavity always contains small stones, which are swallowed by the Bird to aid the gizzard in grinding up the food.

The *duodenum* (*duo.*) leaves the gizzard quite close to the entrance of the proventriculus and forms a distinct loop enclosing the pancreas. The rest of the small intestine is called the *ileum* (*ilm.*): it presents first a single loop, then follows its greater part coiled into a sort of spiral, and lastly comes a single loop which passes without change of diameter into the *rectum* (*rct.*), the junction between the two being marked only by a pair of small blind pouches or *cœca* (*cœ.*). The *cloaca* is a large chamber divided into three compartments, the *coprodæum* (*cpdm.*), which receives the rectum, the *urodæum* (*urdm.*), into which the urinary and genital ducts open, and the *proctodæum* (*prdm.*), which opens externally by the anus.

There are small *buccal glands* opening into the mouth, but none that can be called salivary. The *liver* (*lr.*), is large, and is divisible into right and left lobes, each opening by its own duct (*b. d. 1*, *b. d. 2*), into the duodenum: there is no gall bladder. The *pancreas* (*pn.*) is a compact reddish gland lying in the loop of the duodenum

into which it discharges its secretion by three ducts (*pn. d. 1–3*). A thick-walled glandular pouch, the *bursa Fabricii* (*b. fabr.*), lies against the dorsal wall of the cloaca in young Birds and opens into the proctodæum : it atrophies in the adult.

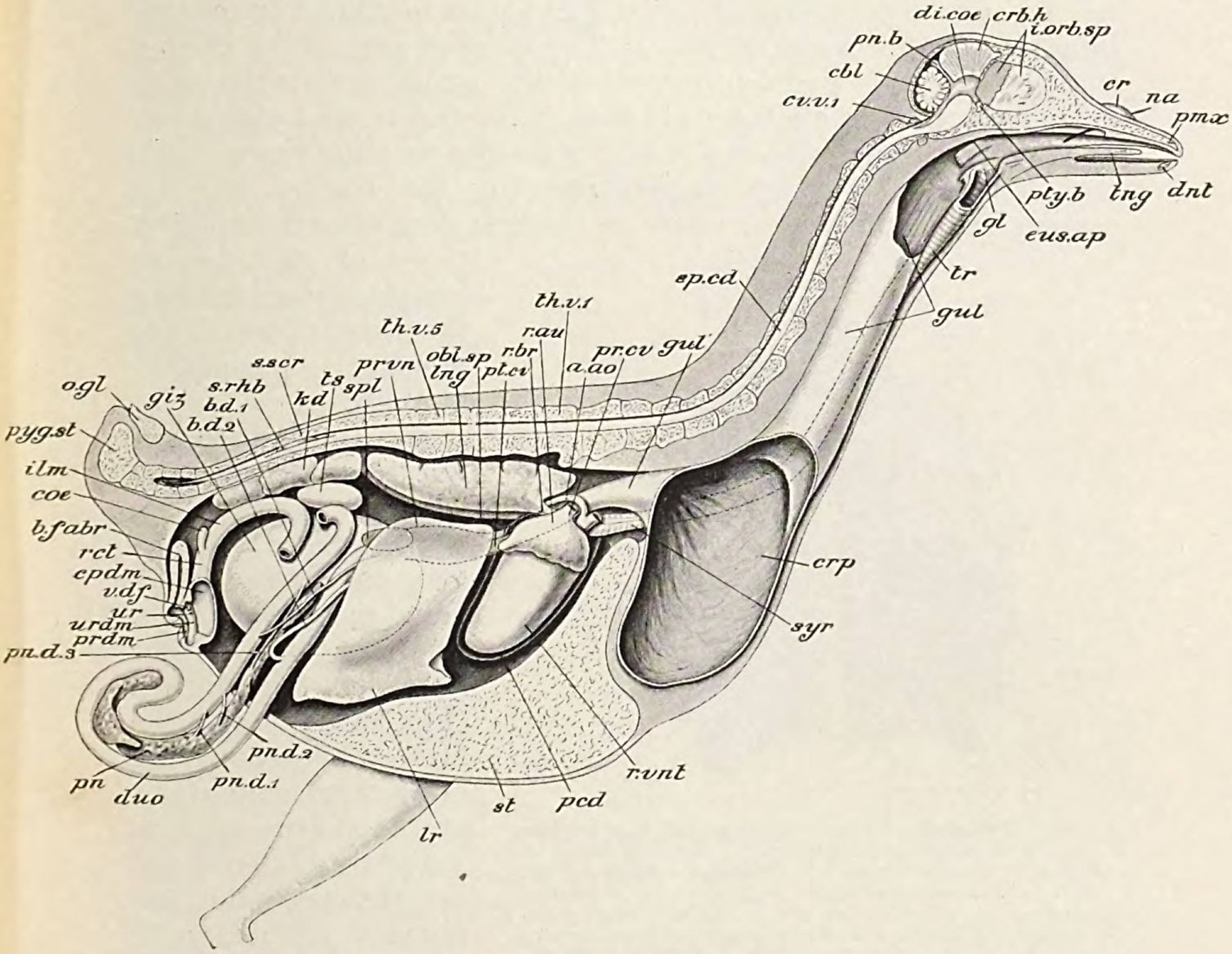


FIG. 981.—**Columba livia.** Dissection from the right side. The body-wall, with the vertebral column, sternum, brain, &c., are in sagittal section ; portions of the gullet and crop are cut away and the cloaca is opened ; nearly the whole of the ileum is removed, and the duodenum is displaced outwards. *a. ao.* aortic arch ; *bd.* 1, *bd.* 2, bile-ducts ; *b. fabr.* bursa Fabricii ; *cbl.* cerebellum ; *cœ.* right cœcum ; *cpdm.* coprodæum ; *cr.* cere ; *crb. h.* left cerebral hemisphere ; *crp.* crop ; *cr. v. 1*, first cervical vertebræ ; *di.cœ.* diacœle ; *dnt.* dentary ; *duo.* duodenum ; *eus. ap.* aperture of Eustachian tubes ; *giz.* gizzard (dotted behind the liver) ; *gl.* glottis ; *gul.* gullet ; *ilm.* ileum ; *i. orb. sp.* inter-orbital septum ; *kd.* right kidney ; *lng.* right lung ; *lr.* liver (right lobe) ; *na.* bristle passed from nostril into mouth ; *obl. sep.* oblique septum ; *o. gl.* oil-gland ; *pcd.* pericardium ; *pmx.* pre-maxilla ; *pn.* pancreas ; *pn. b.* pineal body ; *pnd. 1—3*, pancreatic ducts ; *pr. cv.* right pre-caval ; *prdm.* proctodæum ; *prvn.* proventriculus (dotted behind liver) ; *pt. cv.* post-caval ; *pty. b.* pituitary body ; *pyg.st.* pygostyle ; *r. au.* right auricle ; *r. br.* right bronchus ; *rct.* rectum ; *r. vnt.* right ventricle ; *sp. cd.* spinal cord ; *spl.* spleen (dotted behind liver) ; *s. rhb.* sinus rhomboidalis ; *s. scr.* synsacrum ; *st.* carina sterni ; *syr.* syrinx ; *th. v. 1*, first, and *th. v. 5*, fifth thoracic vertebra ; *tng.* tongue ; *tr.* trachea ; *ts.* right testis ; *ur.* aperture of left ureter ; *urdm.* urodæum ; *v. df.* aperture of left vas deferens.

Ductless Glands.—The *spleen* (*spl.*) is an ovoid red body, of unusually small proportional size, attached by peritoneum to the right side of the proventriculus. There are paired *thyroids* at the base of the neck and, in young Pigeons, there is an elongated

thymus on each side of the neck. The *adrenals* (Fig. 990, *adr.*) are irregular yellow bodies placed at the anterior ends of the kidneys.

Respiratory and Vocal Organs.—The *glottis* (Fig. 981, *gl.*), is situated just behind the root of the tongue, and leads into the *larynx*, which is supported by cartilages—a ventral *thyroid*, a dorsal *cricoid*, and paired *arytenoids*—but does not, as in other Vertebrates, function as the organ of voice. The anterior part of the trachea (*tr.*) has the usual position, ventral to the gullet, but further back it is displaced to the left by the crop, becoming ventral once more as it enters the body-cavity, where it divides into the right (*r. br.*) and left *bronchi*. The rings supporting the trachea are not cartilaginous but bony, as also is the first ring of each bronchus, those of the trachea completely surrounding the tube, those of the bronchi incomplete mesially.

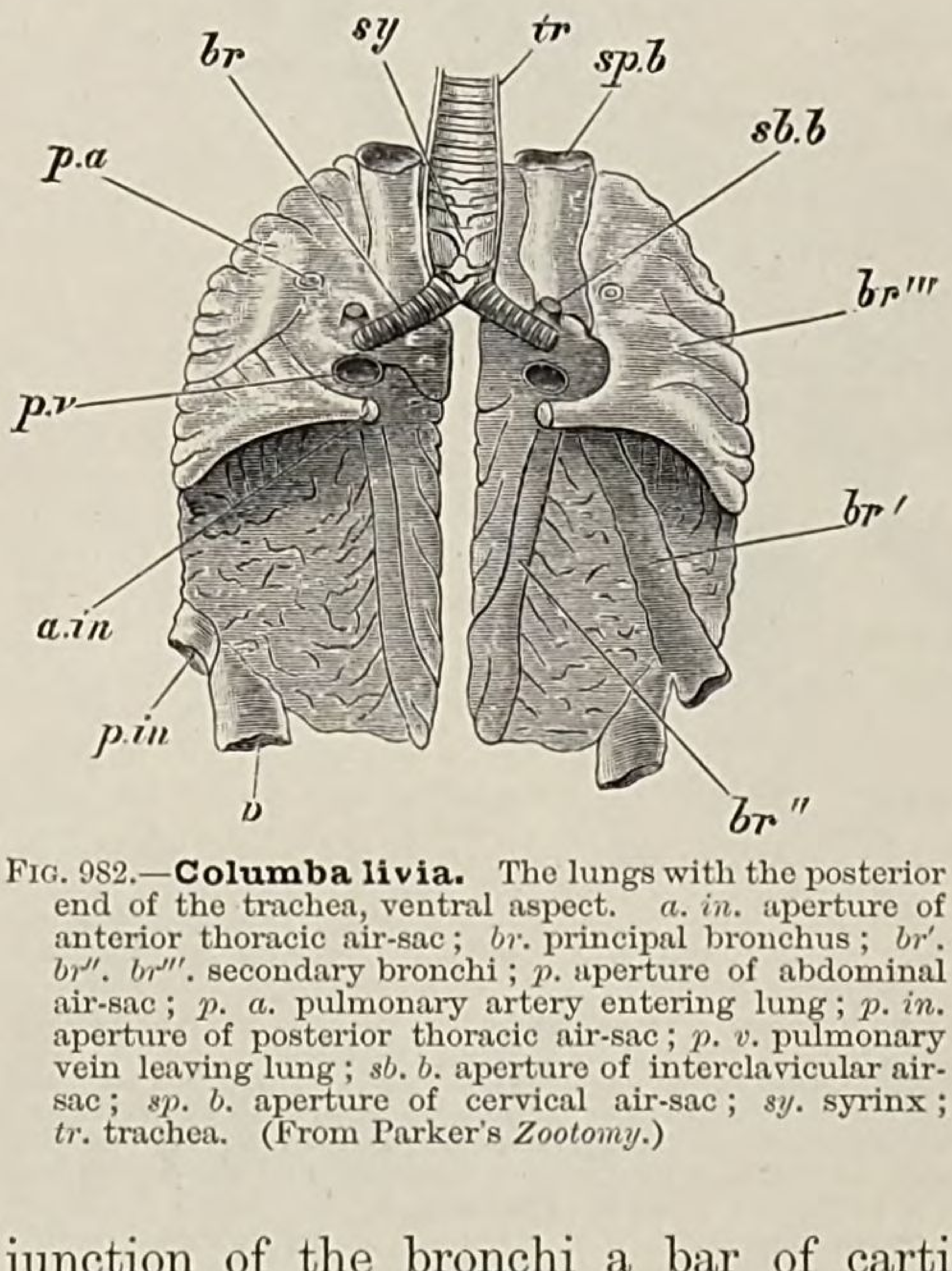


FIG. 982.—**Columba livia.** The lungs with the posterior end of the trachea, ventral aspect. *a. in.* aperture of anterior thoracic air-sac; *br.* principal bronchus; *br'.* *br''.* *br'''.* secondary bronchi; *p.* aperture of abdominal air-sac; *p. a.* pulmonary artery entering lung; *p. in.* aperture of posterior thoracic air-sac; *p. v.* pulmonary vein leaving lung; *sb. b.* aperture of interclavicular air-sac; *sp. b.* aperture of cervical air-sac; *sy.* syrinx; *tr.* trachea. (From Parker's *Zootomy*.)

At the junction of the trachea with the bronchi occurs the characteristic vocal organ, the *syrinx* (*syr.*), found in no other class. The last three or four rings of the trachea (Fig. 982, *tr.*), and the first or bony half ring of each bronchus (*br.*), are modified to form a slightly dilated chamber, the *tympanum*, the mucous membrane of which forms a cushion-like thickening on each side. At the junction of the bronchi a bar of cartilage, the *pessulus*, extends dorso-ventrally and supports an inconspicuous fold of mucous membrane, the *membrana semilunaris*. The membranous inner walls of the bronchi form the *internal tympaniform membranes*. A pair of *intrinsic syringeal muscles* arise from the sides of the trachea and are inserted into the syrinx, and a pair of *sterno-tracheal muscles* arise from the sternum and are inserted into the trachea. The voice is produced by the vibration of the semilunar membrane: its pitch is altered by changes in the form of the tympanum produced by the action of the muscles.

The *lungs* (Fig. 981, *lng.*) are very small in comparison with the size of the Bird, and are but slightly distensible, being solid spongy

organs, not mere bags with sacculated walls as in Amphibia and many Reptiles. Their dorsal surfaces fit closely into the spaces between the ribs, and have no peritoneal covering, their ventral faces are covered by a strong sheet of fibrous tissue, the *pulmonary aponeurosis* or *pleura* (Fig. 983, B, *pul. ap.*), a special development of the peritoneum. Into this membrane are inserted small fan-like *costo-pulmonary muscles*, which arise from the junction of the vertebral and sternal ribs.

The bronchus, on entering the lung, is continued to its posterior edge (Figs. 982 and 983), where it divides into two branches, each of which enters a bladder-like *air-sac*, formed as a dilatation of the mucous membrane of the bronchus. One of these, the *abdominal air-sac* (Fig. 983, A, *abd. a. s*), lies among the coils of the intestine, the other, or *posterior thoracic air-sac* (*post. th. a. s*), is closely applied to the side-walls of the body. The bronchus also gives off, near its entrance into the lung, three short branches, one of which becomes connected with an *anterior thoracic air-sac* (*ant. th. a. s*), situated just in front of the posterior thoracic; another with an *interclavicular air-sac* (*int. clav. a. s*), which is median and unpaired, and connected with both lungs; the third enters a *cervical air-sac* (*cerv. a. s*) placed at the root of the neck. Each side of the interclavicular gives off an *axillary air-sac*, lying in the arm-pit. All these sacs are paired except the interclavicular, which is formed by the fusion of right and left moieties. The sacs are in communication with the pneumatic cavities of the bones.

The ventral or free walls of the thoracic air-sacs of each side are covered by a sheet of fibrous tissue, the *oblique septum* (*obl. sept.*) which is continued forwards to the pericardium, and is united with its fellow of the opposite side in the middle dorsal line: it divides the cœlome into two compartments; one containing the lungs with the interclavicular and thoracic air-sacs, the other (*abd. cav.*) the heart, liver, stomach, intestine, etc., with the abdominal air-sacs.

Besides the branches to the air-sacs the main bronchus gives off secondary bronchi, and these branch again, sending off tubes which end blindly near the surface of the lung and give off blind dilatations commonly know as *alveoli*. The ultimate branches are given off at right angles from those of a higher order.

When the Pigeon is standing, the alternate elevation and depression of the sternum, produced partly by the abdominal, partly by the intercostal muscles, causes an alternate enlargement and diminution of the capacity of the cœlome, and thus pumps air in and out of the lungs. During flight, when the weight is supported by the wings, and the sternum is thus rendered relatively immovable, the same effect seems to be produced by the elevation and depression of the back. In either case the inspired air rushes through the lungs into the air-sacs and thence by diffusion

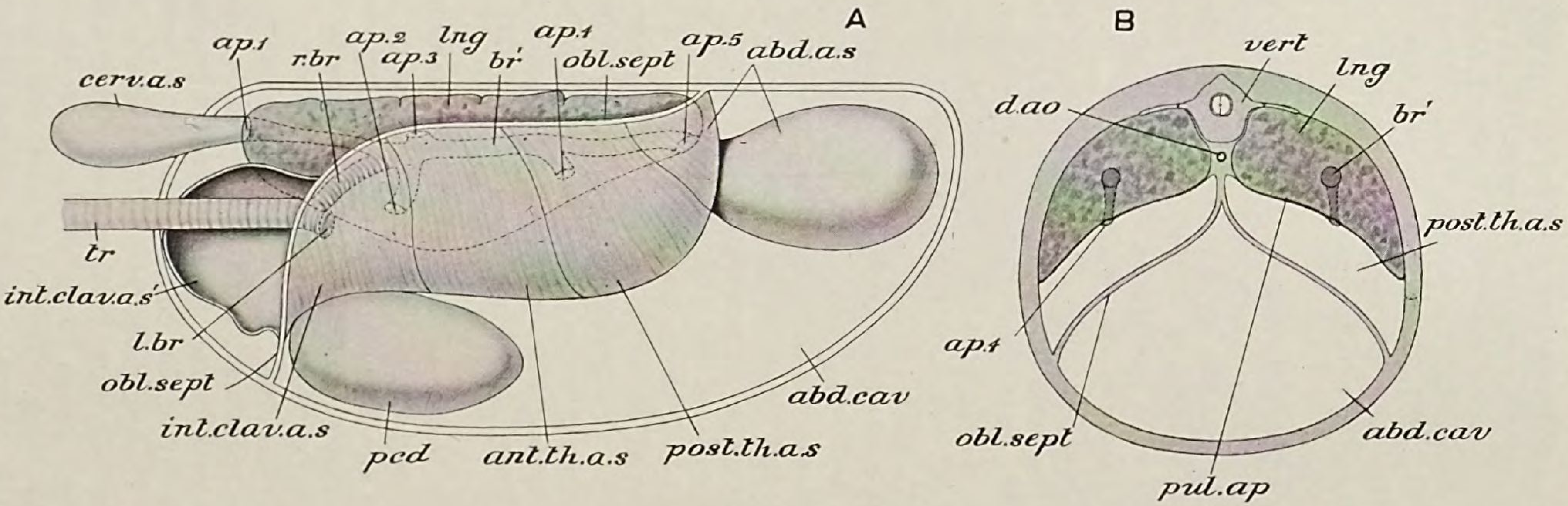


FIG. 983.—Diagrams showing the relations of the air-sacs of a **Bird**. A, from the left side; B, in transverse section; *abd. a. s.* right abdominal air-sac; *abd. cav.* abdominal cavity; *ant. th. a.s.* anterior thoracic air-sac; *ap. 1*, aperture of cervical air-sac; *ap. 2*, of inter-clavicular; *ap. 3*, of anterior thoracic; *ap. 4*, of posterior thoracic; *ap. 5*, of abdominal; *br'.* right bronchus passing through the lung (dotted); *cerv. a. s.* cervical air-sac; *d. ao.* dorsal aorta; *int. clav. a.s.* inter-clavicular air-sac; *int. clav. a. s'.* its anterior portion cut open; *l. br.* left bronchus, cut off short; *lng.* right lung, the outline dotted where it is concealed by the air-sacs; *obl. sept.* oblique septum, the cut edge in A shows the junction of the right and left moieties; *pcd.* pericardium; *post. th. a. s.* posterior thoracic air-sac; *pul. ap.* pulmonary aponeurosis; *r. br.* right bronchus; *tr.* trachea; *vert.* vertebra.

into the pneumatic cavities of the bones. Thus, while in other animals a certain amount of unchanged or residual air is always left in the lungs after each expiration, in Birds the residual air is confined to the air-sacs and to the smaller branches of the bronchi, every respiratory movement drawing a current of fresh or tidal air through the lungs. As a result of this the aëration of the blood is very complete and its temperature correspondingly high. It is worthy of notice that Birds agree with Insects, the only other typically aërial class, in having the inspired air distributed all over the body so that the aëration of the blood is not confined to the limited area of an ordinary respiratory organ.

Circulatory Organs.—The *heart* (Fig. 981, *ht.*) is of great proportional size, and, like that of the Crocodile, consists of four

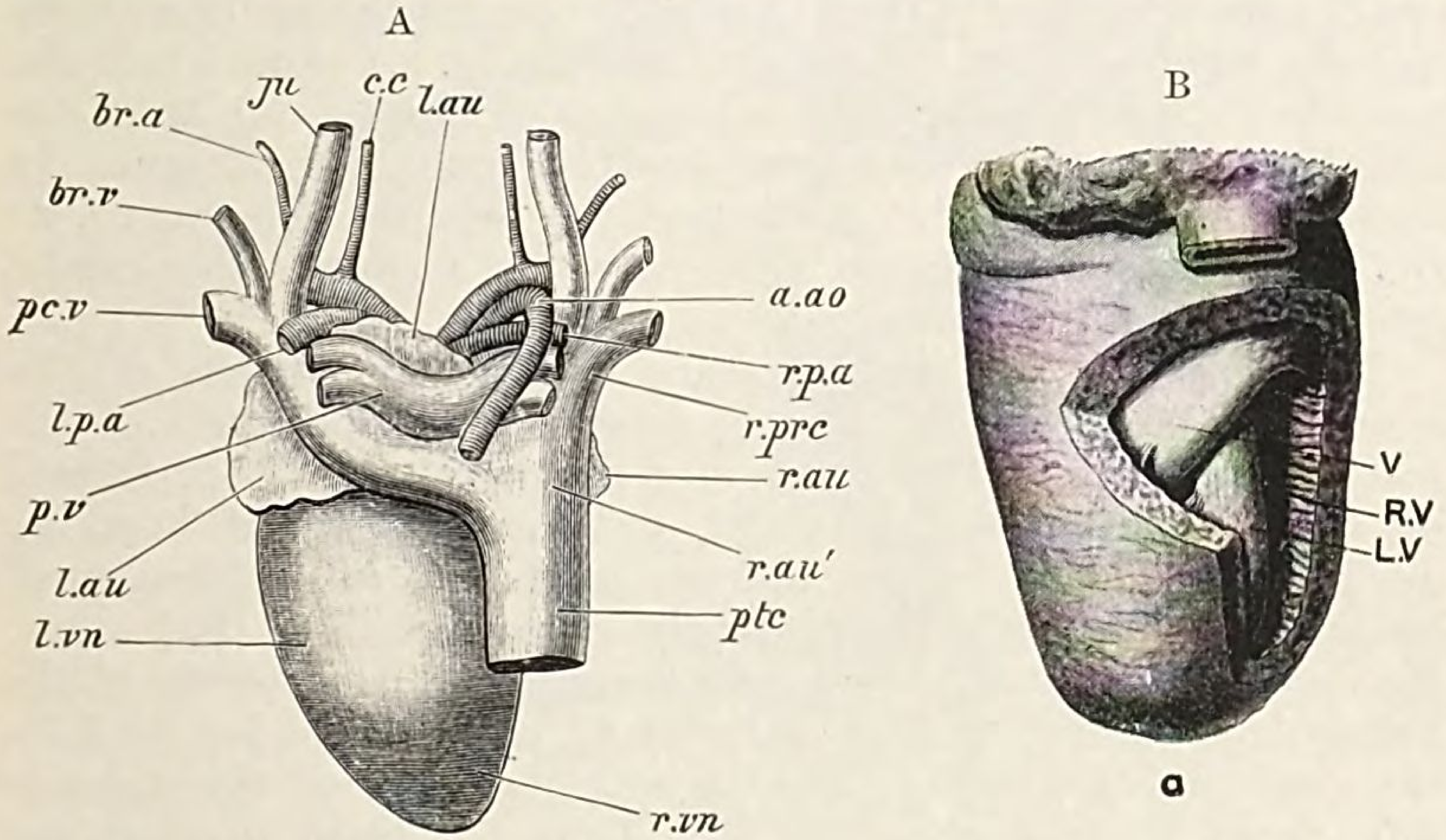


FIG. 984.—A, heart of the **Pigeon**, dorsal aspect. *a. ao.* arch of aorta; *br. a.* brachial artery; *br. v.* brachial vein; *c. c.* common carotid; *ju.* jugular; *l. au.* left auricle; *l. p. a.* left pulmonary artery; *l. vn.* left ventricle; *pc. v.* left pre-caval; *ptc.* post-caval; *p. v.* pulmonary veins; *r. au. r. au′.* right auricle; *r. p. a.* right pulmonary artery; *r. prc.* right pre-caval; *r. vn.* right ventricle. B, heart of a **Bird** with the right ventricle opened; L. V. septum ventriculorum; R. V. right ventricle; V. right auriculo-ventricular valve. (A, from Parker's *Zootomy*; B, from Headley's *Birds*.

chambers, right and left auricles, and right and left ventricles. There is no sinus venosus, that chamber being, as it were, absorbed into the right auricle (Fig. 984, A, *r. au.*). The right ventricle (Fig. 984, B) partly encircles the left, the former having a crescentic, the latter a circular cavity in transverse sections. The left auriculo-ventricular valve has the usual membranous structure, consisting of two flaps connected with the wall of the ventricle by tendons, but the corresponding valve of the right side (R. V.) is a large muscular fold, very characteristic of the class.

The right auricle receives the right and left pre-cavals (*r. prc.*,

pc. v.) and the post-caval (*ptc.*), the left, four large pulmonary veins (*p. v.*). The left ventricle (Fig. 985, *l. vn.*), as in the Crocodile, gives origin to the right aortic arch (*a. ao.*), but the right ventricle (*r. vn.*) gives off only one trunk, the pulmonary artery, which soon divides into two (*r.p.a.*, *l.p.a.*). The left aortic arch is absent in the adult, and it is the right alone which is continued into the dorsal aorta. The result of this is that the systemic arteries receive pure arterial blood from the left side of the heart, and the only mingling of aërated and non-aërated blood is in the capillaries. This is perhaps the most important physiological advance made by Birds over Reptiles.

The aortic arch curves over the right bronchus to reach the dorsal body-wall, and then passes directly backwards as the dorsal aorta (*d. ao.*) Owing to the immense size of the pectoral muscles the arteries supplying them are of corresponding dimensions, and the right and left *innominate arteries* (*in. a.*), from which the carotids (*c. c.*), subclavians (*br. a.*), and pectorals (*pc. a.*), arise, are actually larger than the aorta itself beyond their origin. In correspondence with the position of the legs, the femoral (*f. a.*) and sciatic (*sc. a.*) arteries arise very far forward: the caudal artery (*c.*) is naturally small.

The most characteristic feature in the disposition of the circulatory organs is the almost complete disappearance of the *renal portal system*. There are two renal portal veins (*r. p.*) formed by the bifurcation of the caudal, but each, instead of breaking up into capillaries in the kidney, sends off only a few small branches (*a. r. v.*) which apparently carry blood to that organ, the main vein passing forwards, through the substance of the kidney, and joining the femoral vein (*f. v.*) from the leg to form the iliac vein (*i. v.*) which, uniting with its fellow of the opposite side, forms the post-caval (*pt. c.*). Thus the main part, at any rate, of the blood from the caudal and pelvic regions is taken directly to the heart, and not through the renal capillaries as in most Fishes and all Amphibia and Reptiles.

At the point of bifurcation of the caudal veins a large *coccygeo-mesenteric vein* (*c. m. v.*) gives off, and, running parallel with the rectum, from which it receives tributaries, joins the portal vein. The abdominal vein of Amphibia and Reptiles appears to be represented, in part at least, by the *epigastric vein* (*epg.*), which returns the blood, not from the ventral body wall, but from the *great omentum*, a fold of peritoneum, loaded with fat, lying ventral to the intestines and gizzard: the epigastric discharges into the hepatic vein.

The red blood corpuscles are oval and nucleated. The temperature of the blood is unusually high—over 38° C. (100° F.)

Nervous System.—The brain (Fig. 986) completely fills the cranial cavity, and is remarkable for its short, broad, rounded form.

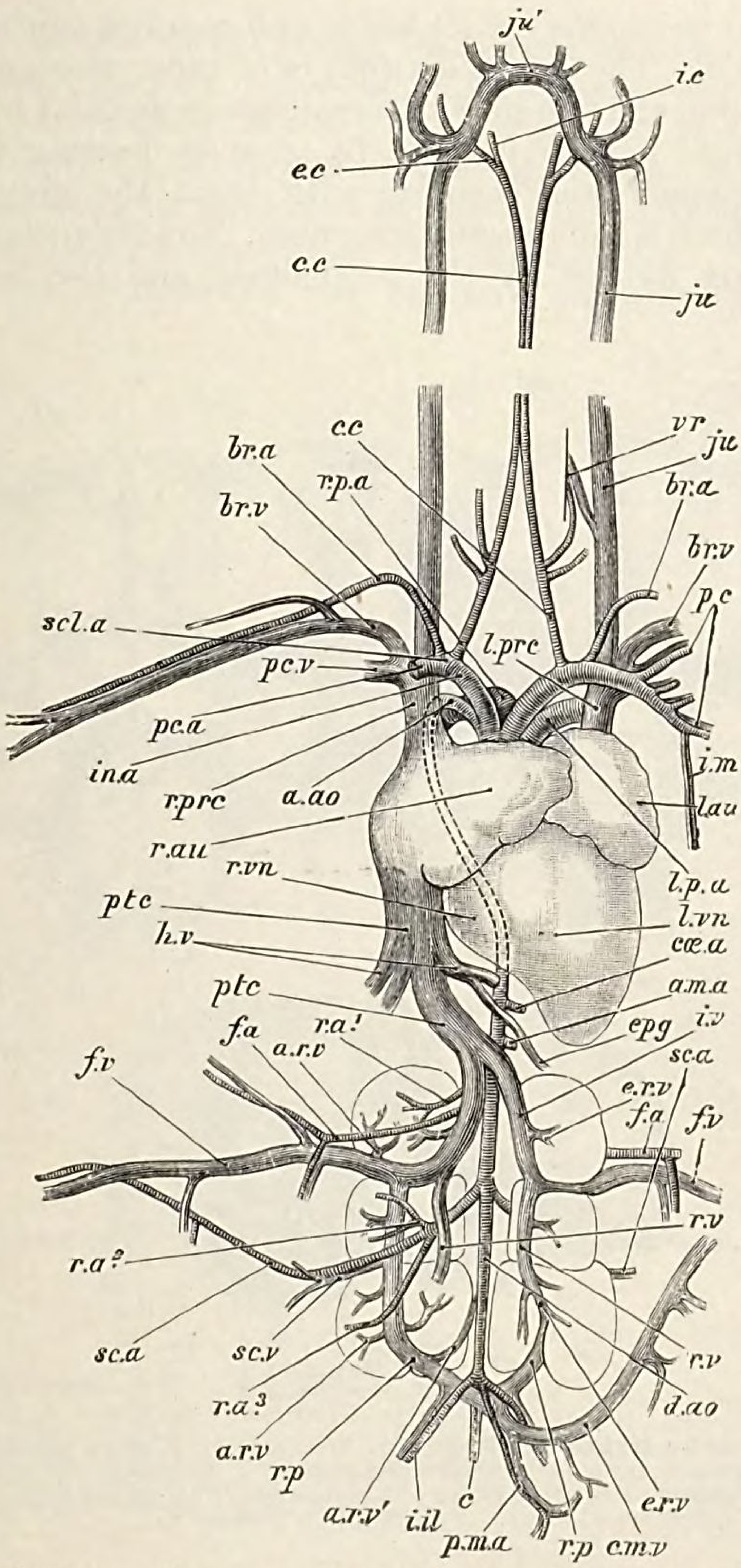


FIG. 985.—**Columba livia**. The heart and chief blood-vessels, ventral aspect] *a. ao.* arch of aorta; *a. m. a.* anterior mesenteric artery; *a. r. v.* afferent renal veins; *a. r. v'.* vein bringing blood from pelvis into renal portal system; *'br. a.* brachial artery; *br. v.* brachial vein; *c.* caudal artery and vein; *c. c.* common carotid artery; *c. m. v.* coccygeo-mesenteric vein, displaced to the right; *cœ. a.* cœliac artery; *d. ao.* dorsal aorta; *e. c.* external carotid artery; *epg.* epigastric vein; *e. r. v.* efferent renal vein; *f. a.* femoral artery; *f. v.* femoral vein; *h. v.* hepatic vein; *i. c.* internal carotid artery; *i. il.* internal iliac artery and vein; *i. m.* internal mammary artery and vein; *in. a.* innominate artery; *i. v.* iliac vein; *ju.* jugular vein; *ju'.* anastomosis of jugular veins; *l. au* left auricle; *l. p. a.* left pulmonary artery; *l. pre.* left pre-caval vein; *l. vn.* left ventricle; *pc.* left pectoral arteries and veins; *pc. a.* right pectoral artery; *pc. v.* right pectoral vein; *p. m. a.* posterior mesenteric artery; *ptc.* post-caval vein; *ra.* 2, *ra.* 2, *ra.* 3, renal arteries; *r. au.* right auricle; *r. p. v.* renal portal vein, on the left side of the figure, supposed to be dissected so as to show its passage through the right kidney; *r. p. a.* right pulmonary artery; *r. pr. v.* right pre-caval vein; *r. v.* renal vein; *r. vn.* right ventricle; *sc. a.* sciatic artery; *sc. v.* sciatic vein; *scl. a.* subclavian artery; *vr.* vertebral artery and vein. (From Parker's *Zootomv.*)

The *medulla oblongata* (*m. o.*) has a well-marked ventral flexure, as in the Lizard. The *cerebellum* (*cb.*) is of great size, and has a large median portion and two small lateral lobes or *flocculi* (*f.*); the surface of the middle lobe is marked by grooves passing inwards in a radiating manner and carrying with them the grey matter, the extent of which is thus greatly increased. The *metacœle* (Fig. 987, *v.4*) is completely hidden by the cerebellum, and the latter is solid,

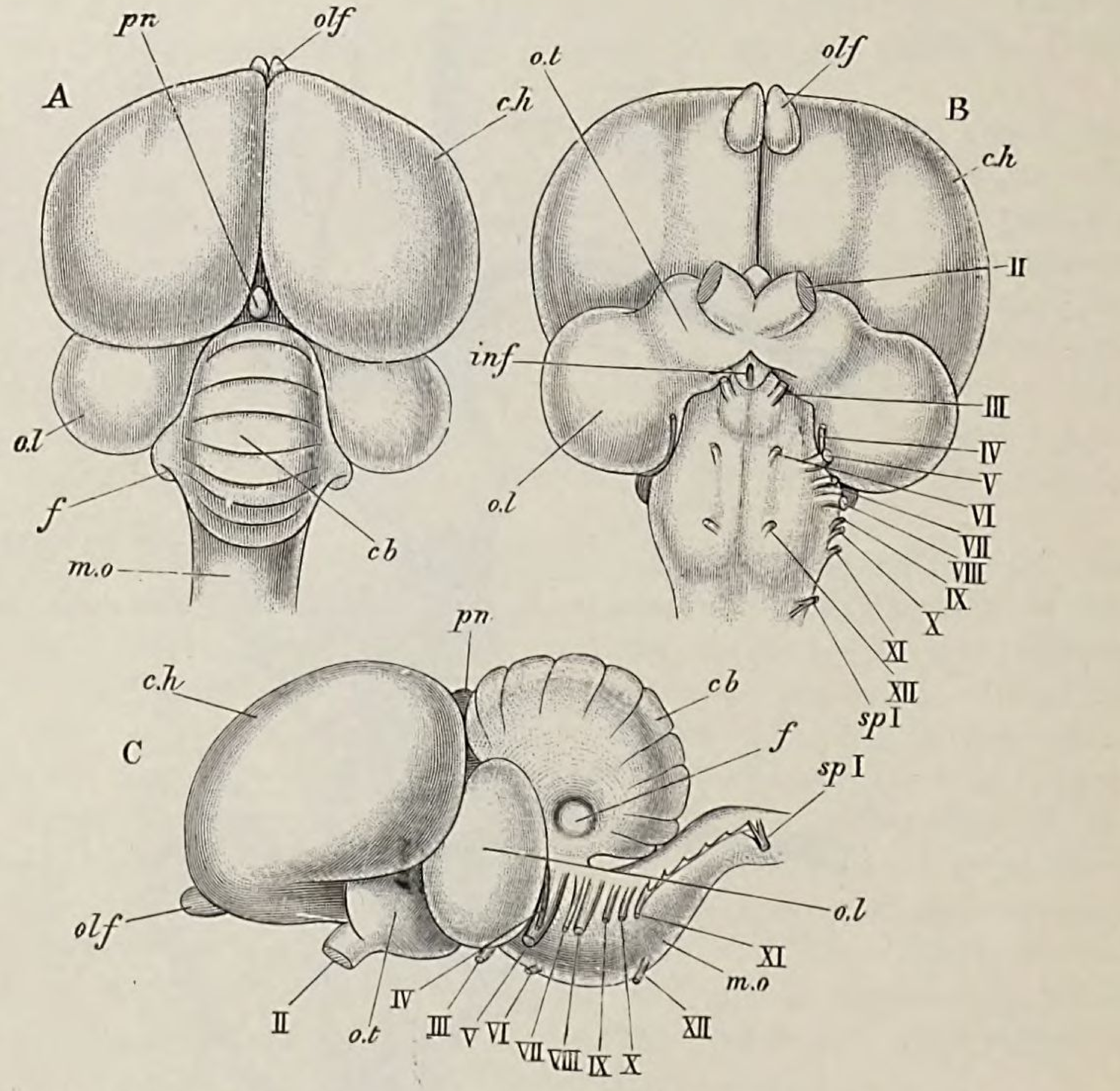


FIG. 986.—**Columba livia.** The Brain; A, from above; B, from below; C, from the left side. *cb.* cerebellum; *c. h.* cerebral hemispheres; *f.* flocculus; *inf.* infundibulum; *m. o.* medulla oblongata; *o. l.* optic lobes; *o. t.* optic tracts; *pn.* pineal body; II—XIII, cerebral nerves; *sp. 1*, first spinal nerve. (From Parker's *Zootomy*.)

having no epicœle. The *hemispheres* (*c. h.*) extend backwards to meet the cerebellum, and the *optic lobes* (*o. l.*) are thereby pressed outwards so as to take up a lateral instead of the usual dorsal position: they are of rounded form, and each contains an *optocœle* (Fig. 987, A, *o. v.*) opening from a narrow passage, the *iter*, which represents the original cavity of the mid-brain. A further result of the extension of the hemispheres and cerebellum respectively backwards and forwards is

that no part of the diencephalon (*thc.*) appears externally except on the ventral surface: elsewhere it is seen only when the hemispheres are pressed aside. It contains a narrow vertical cavity, the *diacœle* (*V.* 3), bounded laterally by the optic thalami, and communicating on each side by the foramina of Monro (*f. m.*) with the *paracœles* or cavities of the hemispheres. The *corpora striata* (*c. s.*) are of immense size, and form the great mass of the

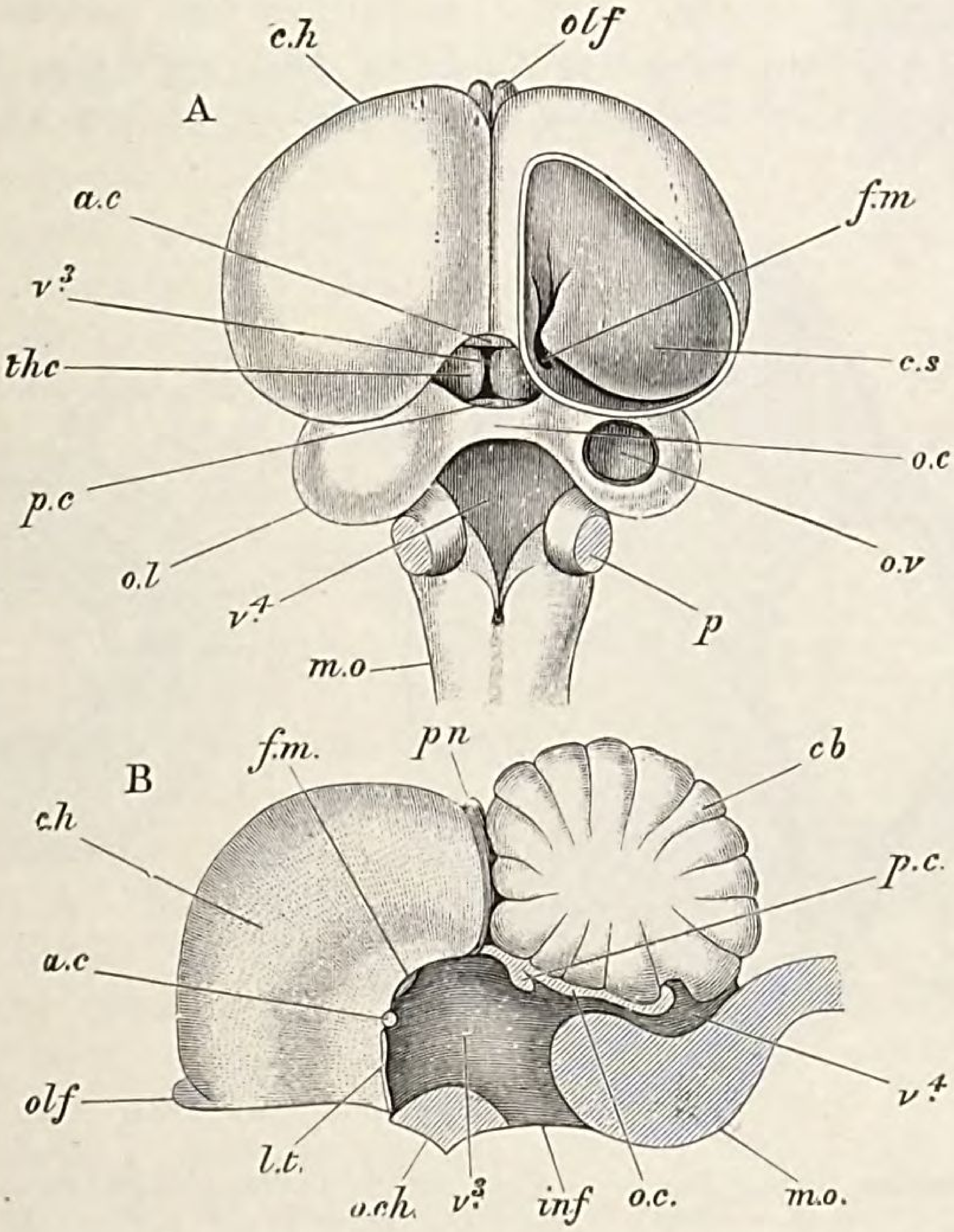


FIG. 987.—**Columba livia.** The brain. A, with the cavities opened from above; B, in sagittal section. *a. c.* anterior commissure; *cb.* cerebellum; *c. h.* cerebral hemispheres; *c. s.* corpus striatum; *f. m.* foramen of Monro; *inf.* infundibulum; *m. o.* medulla oblongata; *o. c.* optic commissure; *o. ch.* optic chiasma; *o. l.* optic lobes; *o. v.* optocœle; *p.* peduncles of cerebellum; *p. c.* posterior commissure; *pn* pineal body; *thc.* diencephalon; *v. 3*, diacœle; *v. 4*, metacœle. (From Parker's *Zootomy*.)

hemispheres: the dorsal portions of the latter, forming the roofs of the paracœles, are very thin. The *olfactory lobes* (*olf.*) are extremely small, in correspondence with the poorly developed olfactory organ: on the other hand the optic nerves and tracts are of unusual size.

The *spinal cord* (Fig. 981, *sp. cd.*) presents large brachial and lumbar enlargements from which the nerves of the fore and hind limbs respectively are given off. In the lumbar enlargement there is a divergence of the dorsal columns of the cord converting

the central canal into a wide diamond-shaped cavity, the *sinus rhomboidalis* (*s. rhb.*) bounded above only by the membranes of the cord.

Sensory Organs.—The *olfactory organs* are paired chambers in the base of the beak, separated from one another by the mesethmoid and bounded externally by the ectoethmoid. The latter is produced inwards into three scroll-like processes, the *turbinals*, which greatly increase the surface of mucous membrane. The anterior portion of the cavity, including the anterior turbinal, is covered by laminated epithelium and serves as a vestibule; its posterior portion, including the middle and posterior turbinals,

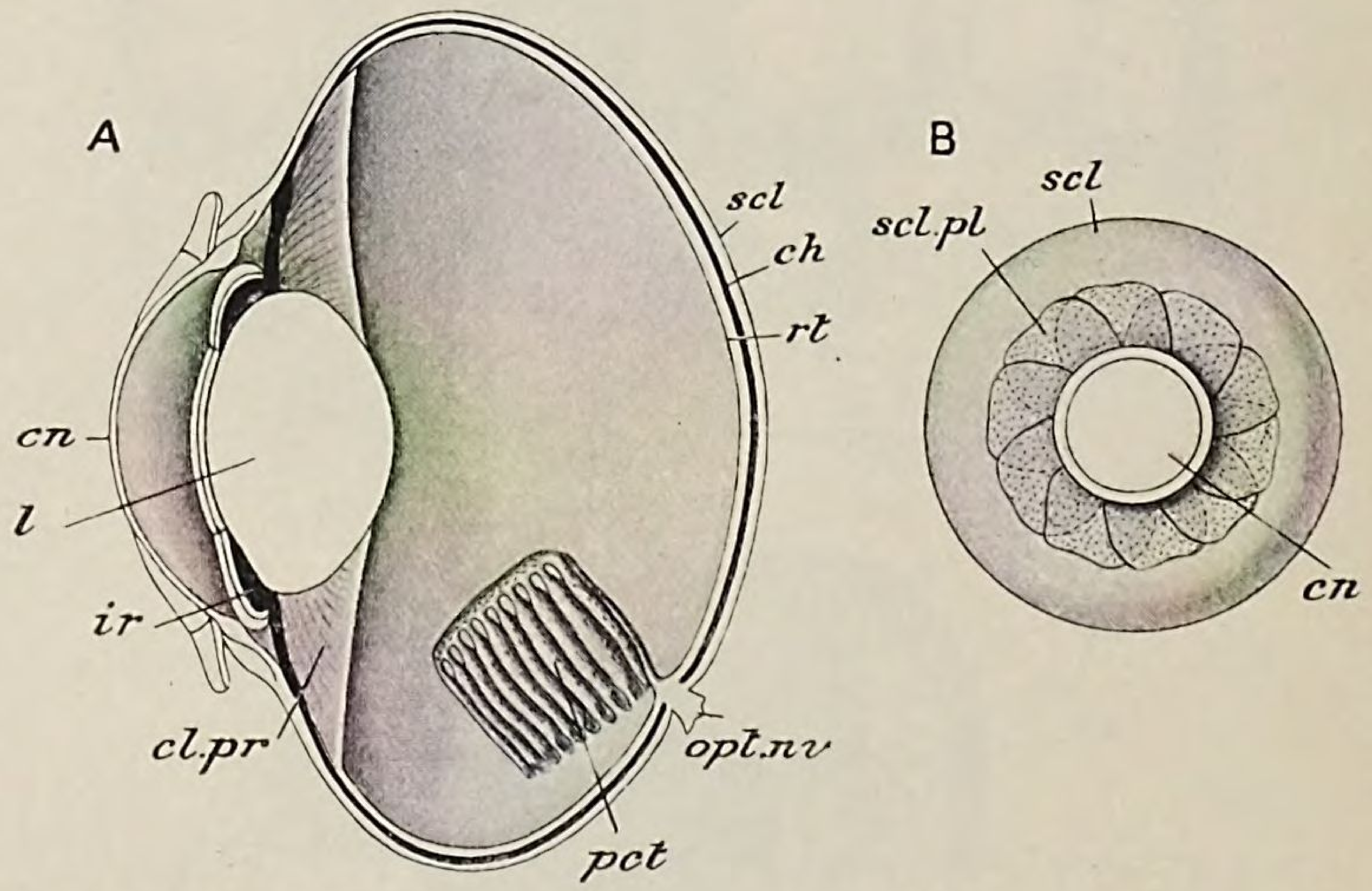


FIG. 988.—**Columba livia.** The eye. A, in sagittal section; B, the entire organ, external aspect. *cn.* cornea; *ch.* choroid; *cl. pr.* ciliary processes; *ir.* iris; *l.* lens; *opt. nv.* optic nerve; *pct.* pecten; *rt.* retina; *scl.* sclerotic; *scl. pl.* sclerotic plates. (After Vogt and Yung.)

is invested by the one-layered epithelium of the Schneiderian membrane to which the fibres of the olfactory nerve are distributed.

The *eye* (Fig. 988) is not even approximately globular, but has the form of a biconvex lens. *Sclerotic plates* (B. *scl. pl.*) are present, and there is a large *pecten* (*pct.*) in the form of a plaited and strongly pigmented membrane projecting into the cavity of the eye from the entrance of the optic nerve.

The *auditory organ* (Fig. 989) is chiefly distinguished from that of Reptiles by the great development of the *cochlea* (*lag.*). The anterior canal (*SB*) is of great size, and the whole membranous labyrinth is closely invested by a layer of dense ivory-like bone,

which can be isolated by cutting away the surrounding spongy bone, and is then seen to form a sort of model of the contained organ, to which the name *bony labyrinth* is applied. The tympanic cavity and columella have the same arrangement as in the Lizard; the narrow eustachian tubes open by a common aperture (Fig. 981, *eus. ap.*) in the roof of the pharynx.

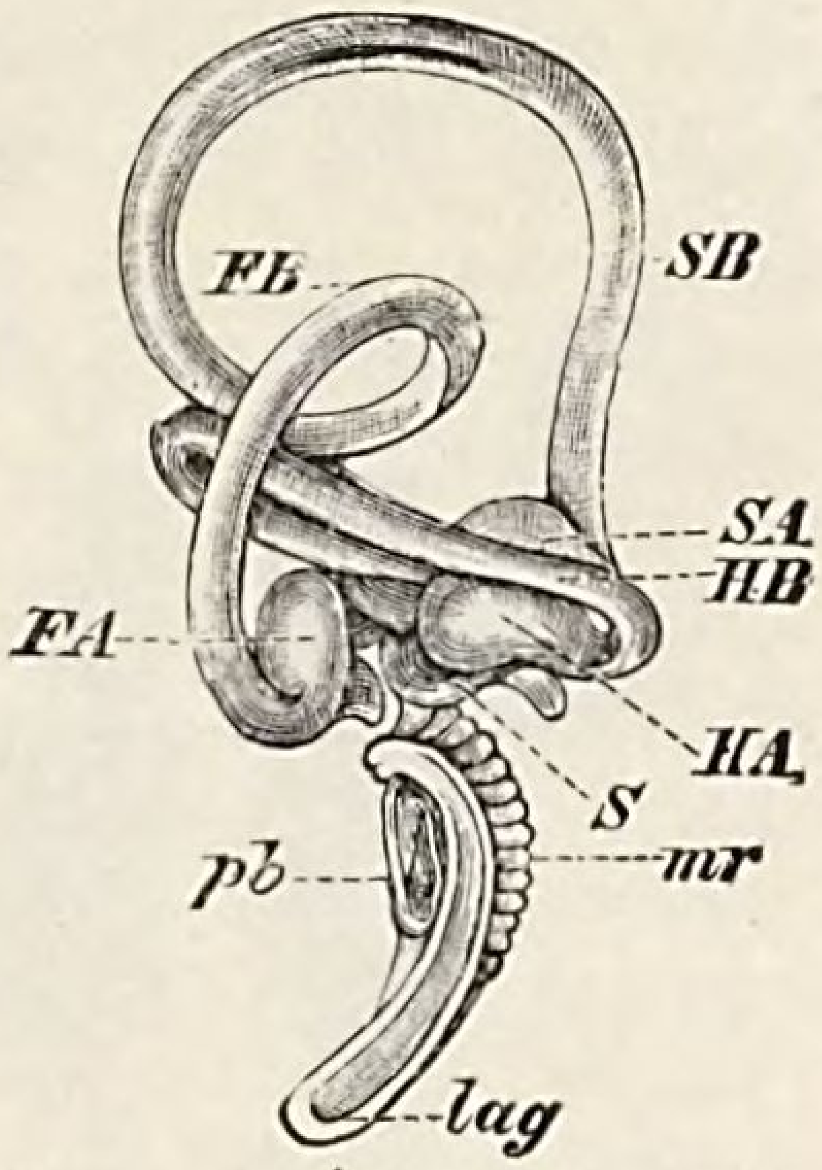


FIG. 989.—**Columba livia.** The right membranous labyrinth, outer aspect. *FA*, ampulla of posterior canal; *FB*, posterior canal; *HA*, ampulla of horizontal canal; *HB*, horizontal canal; *lag.* cochlea or lagena; *mr.* membrane of Reissner; *pb*, basilar part of cochlea; *S.* sacculus; *SA*, ampulla of anterior canal; *SB*, anterior canal. (From Wiedersheim, after Hasse.)

Urinogenital Organs.—The *kidneys* (Fig. 981, *kd*, Figs. 990 and 991, *k*) have a very characteristic form. Each is a flattened organ divided into three main lobes and fitted closely into the hollows of the pelvis. It is formed from the metanephros, the large mesonephros or Wolffian body, which forms the embryonic kidney, undergoing complete atrophy. The *ureters* (*ur.*) are narrow tubes passing directly backwards to open into the urodæum or middle compartment of the cloaca.

The *testes* (Figs. 981 and 990, *ts.*) are ovoid bodies, varying greatly in size according to the season, attached by peritoneum to the ventral surfaces of the anterior ends of the kidneys. From the inner border of each goes off a convoluted *vas deferens* (*vd.*), which passes backwards, parallel with the ureter, to open into the urodæum on the extremity of a small papilla. The posterior end of the spermiduct is slightly enlarged to form a *vesicula seminalis* (*v.s.*). There is no copulatory organ.

The female organs (Fig. 991) are remarkable for the more or less complete atrophy of the right ovary and oviduct. The *left ovary* (*ov.*) is a large organ in the adult Bird, its surface studded with follicles or ovisacs, varying in size from about 15 mm. in diameter downwards, and each containing a single ovum. The *left oviduct* (*l. od.*) is long and convoluted; its anterior end is enlarged to form a wide, membranous cœlomic funnel (*l. od.*″) into which the ripe ova pass on their liberation from the ovisacs; the rest of the tube has thick muscular walls, lined with glandular epithelium, and opens into the urodæum. A fair-sized vestige of the *right oviduct* (*r. od.*) is found in connection with the right side of the cloaca, and a more or less extensive vestige of the *right ovary* is frequently present.

Internal impregnation takes place. As the ova or "yolks" pass down the oviduct they are invested with the secretions of its

various glands; first with layers of *albumen* or "white," next with a parchment-like *shell-membrane*, and lastly with a white calcareous *shell*. They are laid, two at a time, in a rough nest, and are *incubated* or sat upon by the parents for fourteen days, the temperature being in this way kept at about 40° C. (104° F.). At the end of

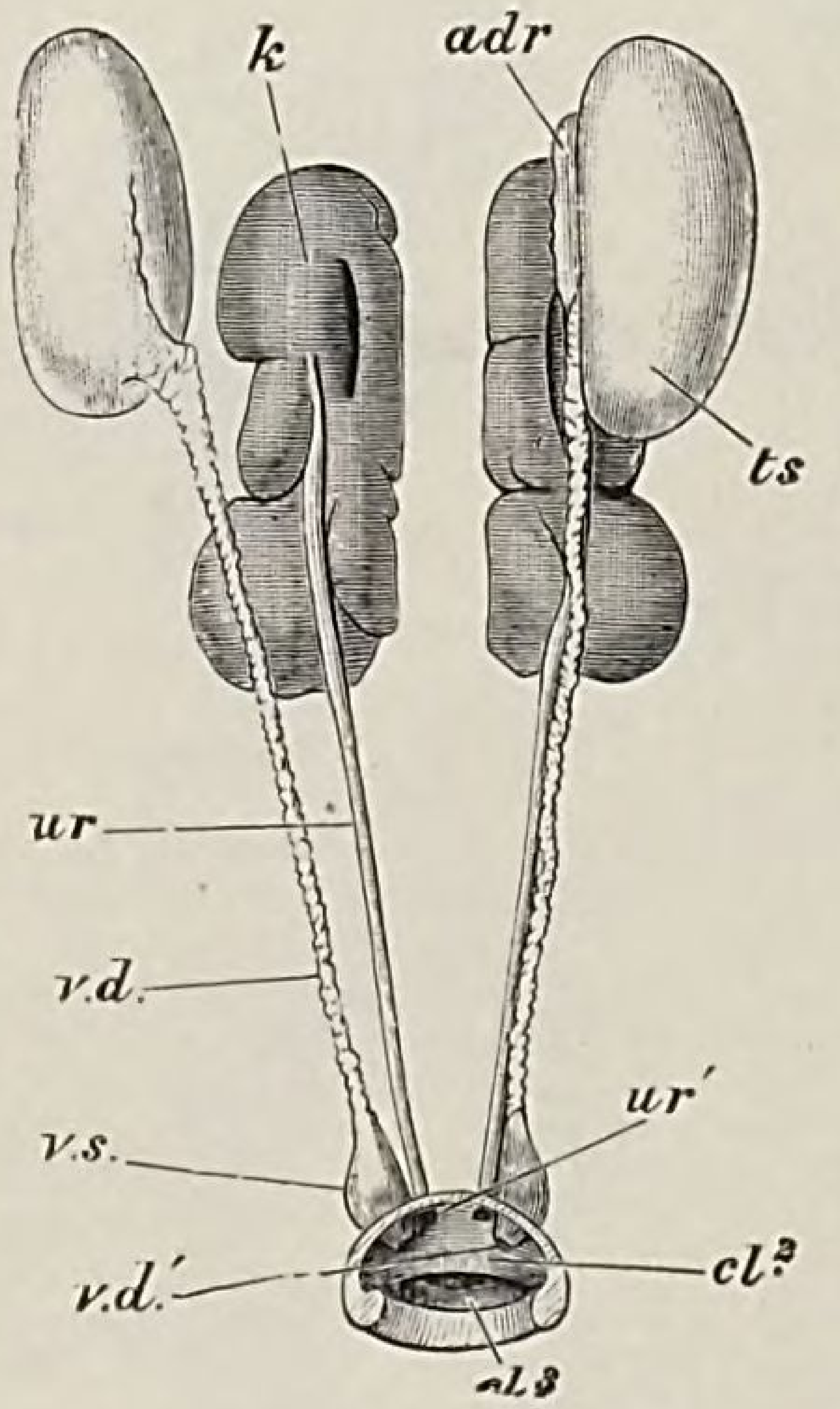


FIG. 990.—**Columba livia.** Male urinogenital organs. *adr.* adrenal; *cl. 2*, urodæum; *cl. 3*, proctodæum; *k.* kidney; *ts.* testis, that of the right side displaced; *ur.* ureter; *ur′.* aperture of ureter; *vd.* vas deferens; *vd′.* its cloacal aperture; *v. s.* vesicula seminalis. (From Parker's *Zootomy*.)

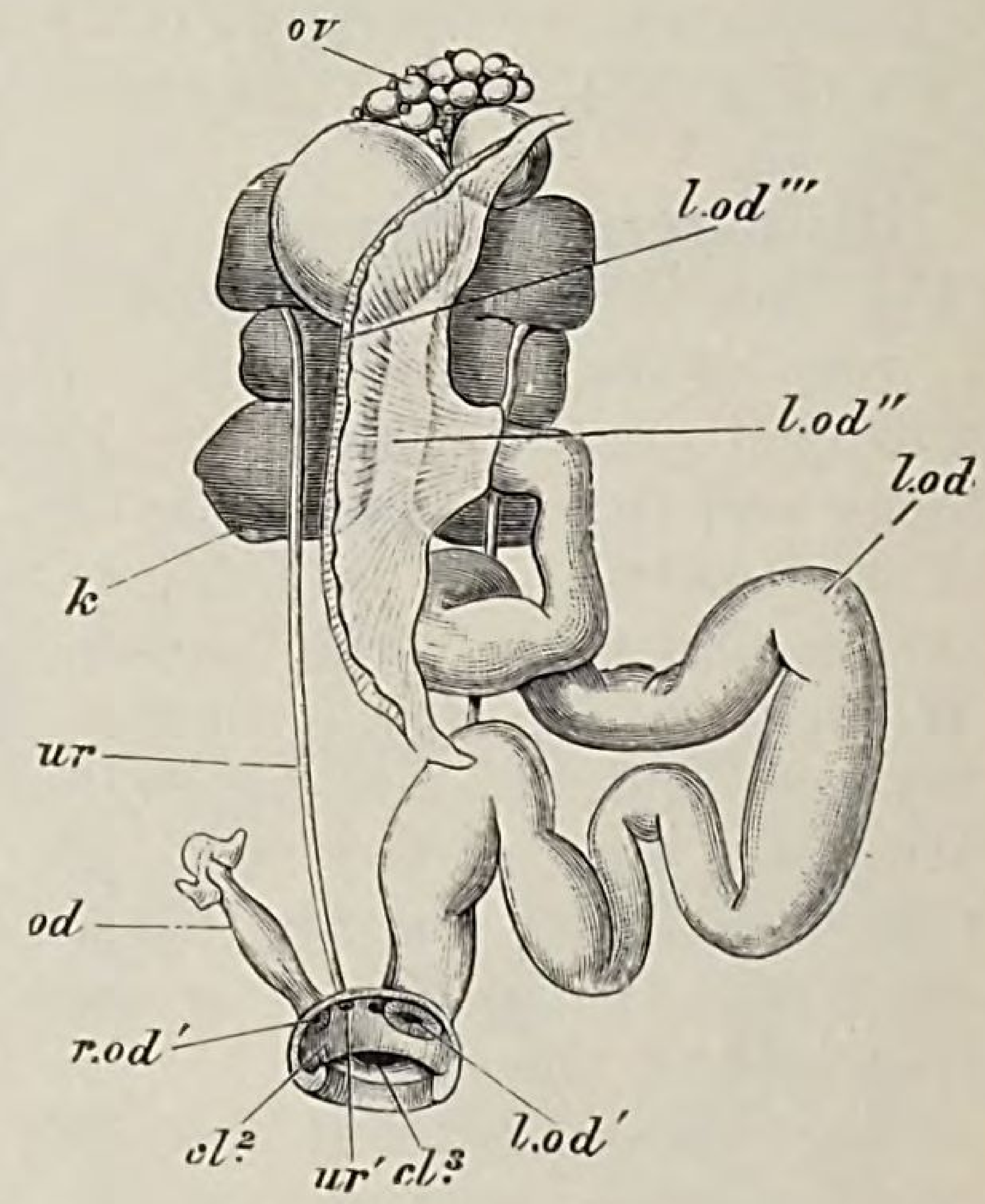


FIG. 991.—**Columba livia.** Female urinogenital organs. *cl. 2*, urodæum; *cl. 3*, proctodæum; *k.* kidney; *l. od.* left oviduct; *l. od′.* its cloacal aperture; *l. od″.* its cœlomic funnel; *l. od‴.* its cœlomic aperture; *ov.* ovary; *r. od.* right oviduct: *r. od′.* its cloacal aperture; *ur.* ureter; *ur′.* its cloacal aperture. (From Parker's *Zootomy*.)

incubation the young Bird is sufficiently developed to break the shell and begin free life. It is at first covered with fine down, and is fed by the parents with a secretion from the crop, the so-called "Pigeon's milk."

2. Distinctive Characters and Classification.

Aves are Craniata in which the epidermal exoskeleton takes the form of feathers over the greater part of the body, of a *rhamphotheca* or horny sheath to the beak, and of claws on the digits of the foot and sometimes of the hand. In the standing position the body is entirely supported on the hind limbs, the articulations of which are thrown forward. The fore-limbs are modified to form wings, usually provided with large feathers for the support of the body during flight. The cervical and free thoracic vertebræ are

usually heterocœlous, but may be procœlous or amphicœlous. The sacral vertebræ are fused with the lumbar and with more or fewer of the posterior thoracic and anterior caudal to form a syn-sacrum for the support of the ilia. The posterior caudal vertebræ are usually fused to form a pygostyle around which the tail-quills are arranged in a semicircle. The bones of the skull undergo early ankylosis. There is a single, rounded, occipital condyle; the united premaxillæ form nearly the whole of the upper jaw; and the lower jaw is composed originally of five or six bones in each ramus, and is supported by a freely articulated quadrate. The vertebral ribs are double-headed, provided with bony uncinates, and articulate with the bony sternal ribs by synovial joints. The sternum is broad, and is typically produced into a longitudinal ventral keel, having a separate centre of ossification. The coracoid is usually more or less pillar-like, the scapula is sabre-shaped, and the clavicles and interclavicle unite to form a furcula. Except in one extinct species the distal carpals and the metacarpals are united to form a carpo-metacarpus. There are usually only three digits in the wing which probably represent the first, second, and third of the typical hand. The ilium is of great size, having large pre- and post-acetabular portions. The acetabulum is perforated in the dry bone. The pubis and ischium are directed backwards and, except in one case of each, there is neither pubic nor ischiadic symphysis. The head of the femur is at right angles to the shaft. The proximal tarsals are fused with the tibia to form a tibio-tarsus; the fibula is much reduced. The distal tarsals are fused with the second, third, and fourth metatarsals to form a tarso-metatarsus; the first metatarsal is free. The fifth digit of the typical foot is absent.

In all tertiary and recent Birds teeth are absent. The gullet is frequently dilated into a crop and the stomach is usually divided into proventriculus and gizzard. The junction between the large and small intestines is marked by a pair of cœca. The lungs are spongy and non-distensible. The bronchi give off branches which open on the surface of the lung into thin-walled air-sacs, and these in their turn communicate with pneumatic cavities in more or fewer of the bones. The voice is produced in a syrinx situated at or near the junction of the trachea with the bronchi. The heart is four-chambered, the right auriculo-ventricular valve is muscular, and the right aortic arch alone is present in the adult. The renal portal system is vestigial. The red blood-corpuscles are oval and nucleated. The temperature of the blood is high (about 38° C.). The optic lobes are displaced laterally owing to the meeting of the large cerebral hemispheres and cerebellum. The lumbar region of the spinal cord has a sinus rhomboidalis. The olfactory organ is usually poorly developed. The eye is usually large, and has sclerotic plates and a pecten. The auditory organ has a large

curved cochlea. The kidney is three-lobed, and is developed from the metanephros, the mesonephros undergoing atrophy. There is no urinary bladder. The ovary and oviduct of the right side are more or less completely atrophied.

Birds are all oviparous, and the large ovum, containing much food-yolk, becomes invested with albumen, a shell-membrane, and a calcareous shell in its passage down the oviduct. The embryo has an amnion, an allantois, and a large yolk-sac. The newly-hatched young may be either well covered with down and able to run or swim and to obtain their own food, in which case they are said to be *precocious*, or may be more or less naked and dependent for a time upon the parents for their food supply, when they are *non-precocious*.

There is no general agreement with regard to the classification of Birds. Owing to the singular uniformity of the class in essential matters of structure, the vast and bewildering diversity in detail, and the puzzling cross-relationships between group and group, the splitting up of the class into orders is a matter of great difficulty and one upon which hardly two ornithologists are agreed. The following scheme will probably answer the present purpose sufficiently well.

Sub-class I.—Archæornithes.

Mesozoic Birds having no ploughshare bone, but a long tail of many vertebræ, having the rectrices arranged in two rows, one on each side of it. The carpals and metacarpals are probably free and the hand has three clawed digits. Teeth are present in both jaws.

Including the single genus and species *Archæopteryx lithographica*, known only from two fossil specimens found in the Upper Jurassic rocks of Bavaria.

Sub-class II.—Neornithes.

Birds in which the greatly shortened tail usually ends in a pygostyle, around which the rectrices, when present, are arranged in a semicircle. Except in a few extinct forms there are no teeth. The metacarpals are fused with the distal carpals to form a carpo-metacarpus. Except in one instance not more than two digits of the hand bear claws.

Division A.—Ratitæ.

Flightless Neornithes, usually of large size, having no hooked barbules to the feathers, so that the barbs are free. Apteria are usually absent in the adult. The rectrices are absent or irregularly arranged and the pygostyle is small or undeveloped. The sternal

keel is vestigial or absent. The coracoid and scapula are comparatively small and completely ankylosed; the acrocoracoid process is vestigial, and the coraco-scapular angle approaches two right angles. The wing is reduced in size and may be vestigial or absent. There are large basi-pterygoid processes developed from the basisphenoid. The vomer is large and broad. The quadrate articulates with the skull by a single or partially divided facet. The male has a penis. The young are precocious.



FIG. 992.—**Apteryx australis,** with egg. (From a specimen in the Royal College of Surgeons, London.)

ORDER 1.—MEGISTANES.

Including (*a*) the Emus (*Dromæus*) and Cassowaries (*Casuarius*), (*b*) the Kiwis (*Apteryx*, Fig. 992), and (*c*) the Moas (*Dinornithidæ*, Fig. 1007).

ORDER 2.—RHEÆ.

Including the South American Ostriches (*Rhea*).

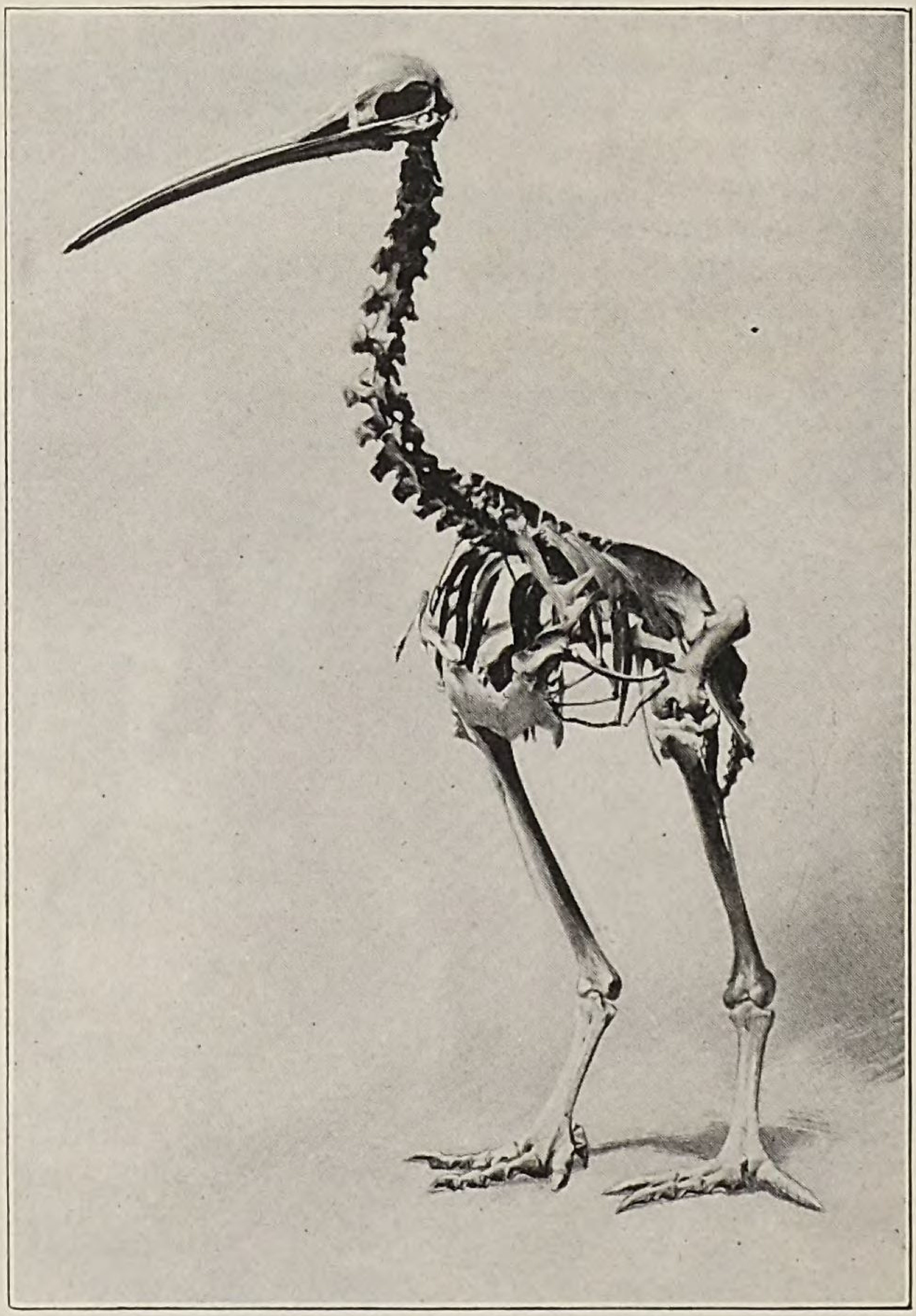


FIG. 992 *bis*.—**Apteryx australis.** Skeleton. (From a specimen in the British Museum—Natural History).

ORDER 3.—STRUTHIONES.

Including the true Ostriches (*Struthio*).

ORDER 4.—ÆPYORNITHES.

Including only the post-pliocene Madagascan genus *Æpyornis.*

ORDER 5.—GASTORNITHES.

Including *Gastornis* and other genera from the Eocene of Europe

Division B.—**Carinatæ.**

Neornithes in which, with the exception of some flightless species the sternum has a keel, the coracoid and scapula are not ankylosed, the acrocoracoid and usually the furcula are well developed, and the coraco-scapular angle is less than a right angle. There is a pygo-

style around which the rectrices are arranged. The quadrate usually articulates with the skull by two facets. The barbs of the feathers have hooklets.[1]

ORDER 1.—STEREORNITHES.[2]

Including *Phororhacos*, *Dryornis*, and other genera from the Eocene of South America.

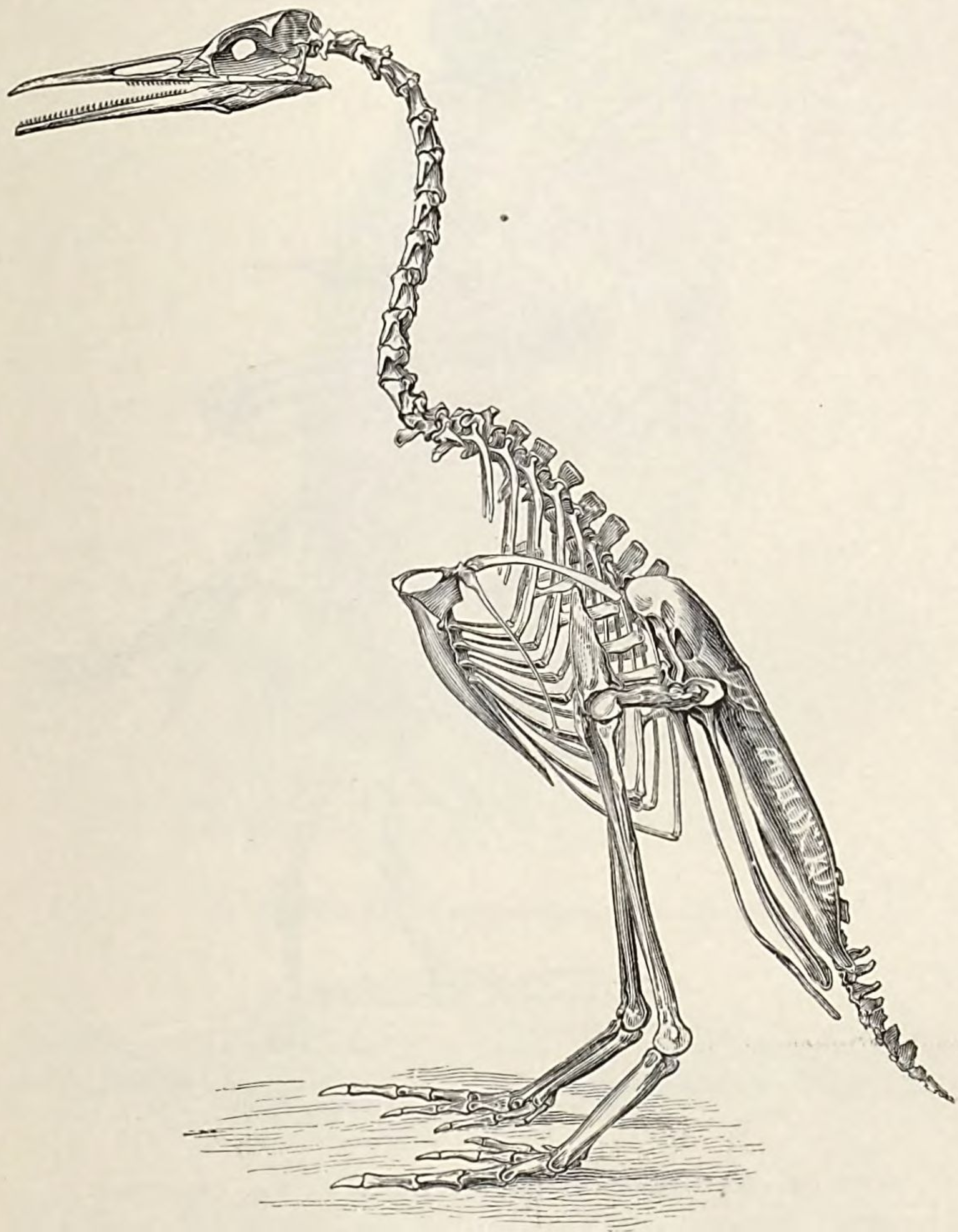


FIG. 993.—**Hesperornis regalis.** The restored skeleton. (After Marsh.)

ORDER 2.—ODONTOLCÆ.

Including *Hesperornis* (Fig. 993), a large diving and swimming Bird, from the Cretaceous of North America, and other less known genera.

[1] Except, perhaps, in Hesperornis.

[2] Recent investigations indicate that this is not a natural group, but that its various genera will have to be distributed amongst other Orders of Carinatæ.

Order 3.—Ichthyornithes

Including *Ichthyornis* (Fig. 994) and *Apatornis*. Tern-like Birds from the Cretaceous of North America.

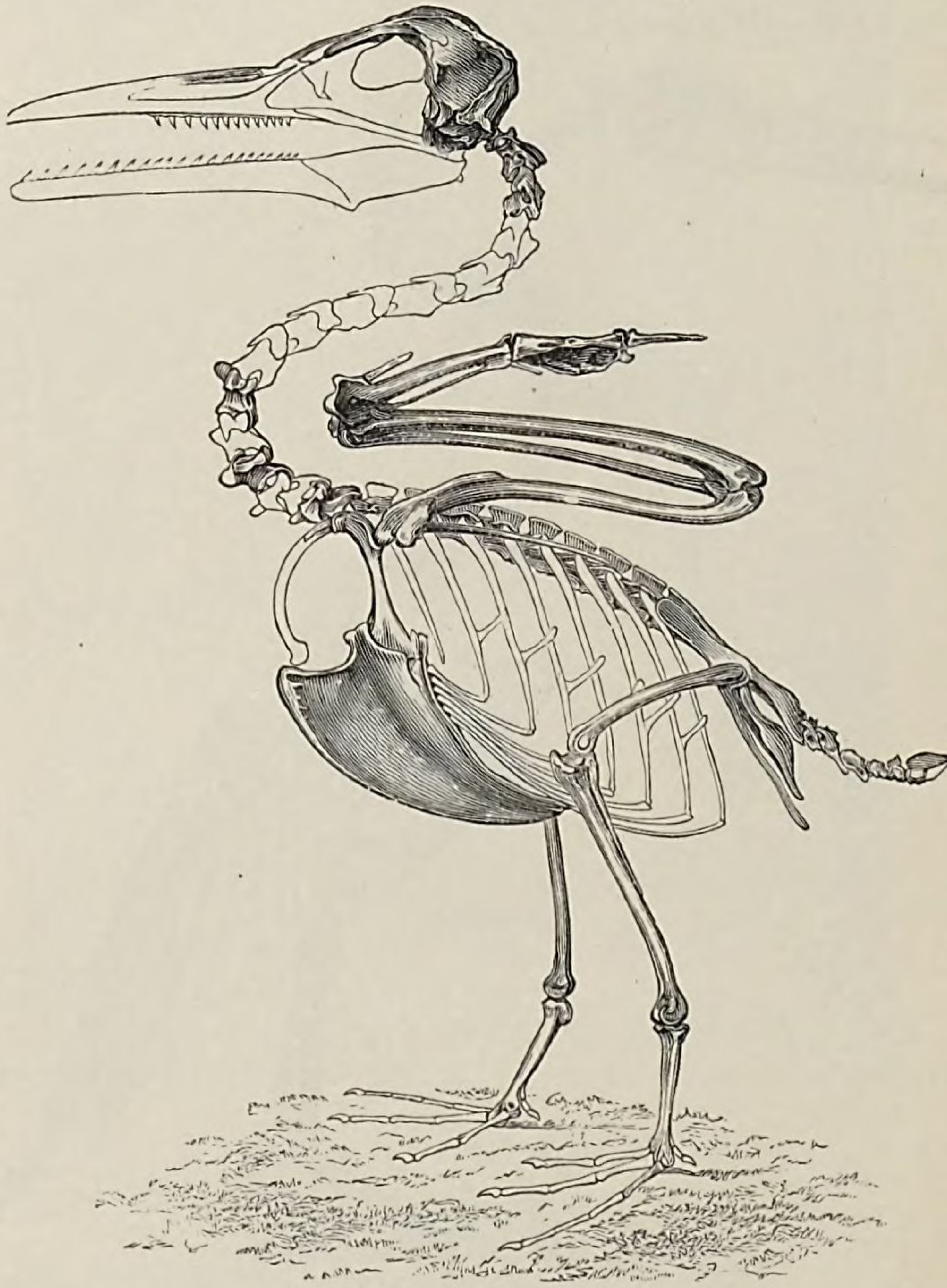


Fig. 994.—**Ichthyornis victor.** The restored skeleton. (After Marsh.)

Order 4.—Pygopodes.

Including the Divers (*Colymbus*) and the Grebes (*Podicipes*).

Order 5.—Impennes.

Including the Penguins (*Aptenodytes*, *Eudyptes*, &c., Fig. 995).

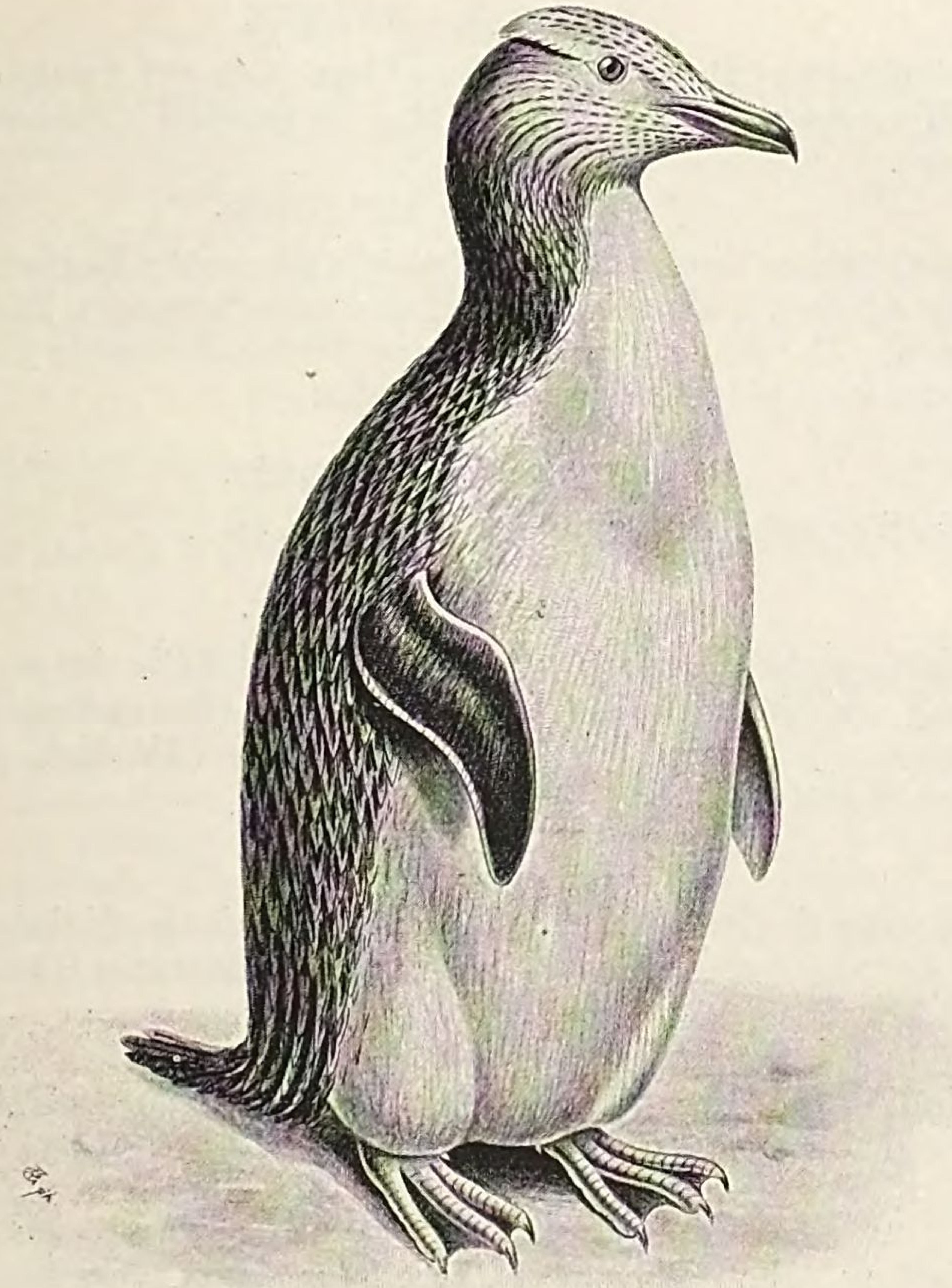


FIG. 995.—**Eudyptes antipodum.** (After Buller.)

ORDER 6.—TURBINARES.

Including the Petrels, such as the Albatrosses (*Diomedea*), Storm-petrels (*Oceanites*), Fulmars (*Fulmarus*), Shearwaters (*Puffinus*), &c.

ORDER 7.—STEGANOPODES.

Including the Boatswain-bird (*Phaëthon*), Gannets (*Sula*), Cormorants or Shags (*Phalacrocorax*), Frigate-bird (*Fregata*), and Pelicans (*Pelecanus*).

ORDER 8.—HERODIONES.

Including the Herons (*Ardea*, &c.), Storks (*Ciconia*, &c.) Ibises (*Ibis*), Spoonbills (*Platalea*), and Flamingoes (*Phœnicopterus*).

ORDER 9.—ANSERES.

Including the Ducks (*Anas*, &c.), Geese (*Anser*), Swans (*Cygnus*), and Mergansers (*Mergus*); and the Screamers (*Palamedea* and *Chauna*).

ORDER 10.—ACCIPITRES.

Including the diurnal Birds of prey, such as the Eagles (*Aquila*), Falcons (*Falco*), Vultures (*Vultur*, &c), and Secretary Bird (*Gypogeranus*). The American Vultures or Turkey-buzzards (*Cathartes*), are sometimes placed in a distinct order.

ORDER 11.—CRYPTURI.

Including only the Tinamous (*Tinamus*, &c.).

ORDER 12.—GALLINÆ.

Including the Fowls (*Gallus*), Pheasants (*Phasianus*), Grouse (*Tetrao*), and other Game Birds; Curassows (*Crax*), Brush-turkeys (*Megapodius*), Hemipodes or Button-quails (*Turnix*), and the Hoatzin (*Opisthocomus*).

ORDER 13.—GRALLÆ.

Including the Rails (*Rallus*, *Ocydromus*, &c.), the flightless Giant Rail (*Aptornis*), the Cranes (*Grus*, &c.), the Bustards (*Otis*), etc.

ORDER 14.—GAVIÆ.

Including the Gulls (*Larus*) and Terns (*Sterna*), and the Auks (*Alca* and *Fratercula*).

ORDER 15.—LIMICOLÆ.

Including the Plovers (*Charadrius*, &c.), Oyster-catchers (*Hæmatopus*), Curlews (*Limosa*), Jacanas (*Parra*), etc.

ORDER 16.—PTEROCLETES.

Including the Sand-grouse (*Pterocles* and *Syrrhaptes*).

ORDER 17.—COLUMBÆ.

Including the Pigeons and Doves (*Columba*, *Turtur*, etc.), Crowned Pigeons (*Goura*), and the extinct flightless Dodo (*Didus*) and Solitaire (*Pezophaps*).

ORDER 18.—PSITTACI.

Including the Parrots (*Psittacus*, &c.), Parrakeets (*Platycercus*), Cockatoos (*Cacatua*), Lories (*Lorius*), and Macaws (*Ara*).

ORDER 19.—STRIGES.

Including the Owls (*Strigidæ*).

Order 20.—Picariæ.

A somewhat heterogeneous group including the Cuckoos (*Cuculidæ*), Plantain-eaters (*Musophagidæ*), Rollers (*Coraciidæ*), Motmots (*Momotidæ*), Kingfishers (*Alcedinidæ*), Bee-eaters (*Meropidæ*), Hoopoes (*Upupidæ*), Goat-suckers (*Caprimulgi*), Swifts (*Cypselidæ*), Humming Birds (*Trochilidæ*), Colies (*Colii*), Trogons (*Trogones*), Woodpeckers and Hornbills (*Pici*), etc.

Order 21.—Passeres.

Including the Lyre-birds (*Menura*), Larks (*Alaudidæ*), Starlings (*Sturnidæ*), Finches (*Fringillidæ*), Swallows (*Hirundinidæ*), Blackbirds and Thrushes (*Turdidæ*), Birds of Paradise (*Paradiseidæ*), Crows (*Corvidæ*), etc.

Systematic Position of the Example.

The numerous species of Columba belong to the family *Columbidæ*, of the order *Columbæ*.

The following are the chief characters of the Columbæ:—there are eleven primary remiges, the first very small; the skull is schizognathous; the oil-gland has no tuft of feathers; the vomer is vestigial; there is a large crop; the cœca are vestigial; and the young are non-precocious.

Of the two families of Columbæ the *Columbidæ*, or Doves and Pigeons, are distinguished from the *Dididæ*, including the Dodo and Solitaire, by the power of flight and the accompanying typical carinate characters of the sternum and shoulder-girdle.

In Columba there are twelve rectrices; the second primary remex is longer than the sixth, and the proximal portion of the tarso-metatarsus is feathered.

3. General Organization.

In respect of range of structural variations, the entire class of Birds is hardly the equivalent of a single order of Reptiles. Among existing Birds the Emu and the Raven, which may be said to stand at opposite ends of the series, present nothing like the anatomical differences to be found between a common Lizard and a Chameleon, or between a Turtle and a Tortoise. Hence in dividing the class into orders we find none of those striking distinctive characters which separate the orders of Fishes, Amphibia, and Reptiles, but have to be content with characters which in other groups would be considered insignificant, such as details in the structure of the skull and sternum, in the arrangement of the muscles of the wing and leg, in the form of the foot, and in the peculiarities of the newly-hatched young. It is for this reason that in the preceding classification no diagnoses of the orders are given: to define them adequately would involve a degree of anatomical detail quite beyond the scope of the present work.

The differences between the two avian sub-classes, the Archæornithes and the Neornithes, are, however, of a far more fundamental nature, and as Archæopteryx, the sole representative of the first of these groups, is a unique form, and perhaps the best example of an undoubted link between two classes—Reptiles and Birds—it will be convenient to deal with it separately.

Sub-Class I.—Archæornithes.

Only two specimens of Archæopteryx have hitherto been found, both in the finely-grained lithographic limestone of Solenhofen,

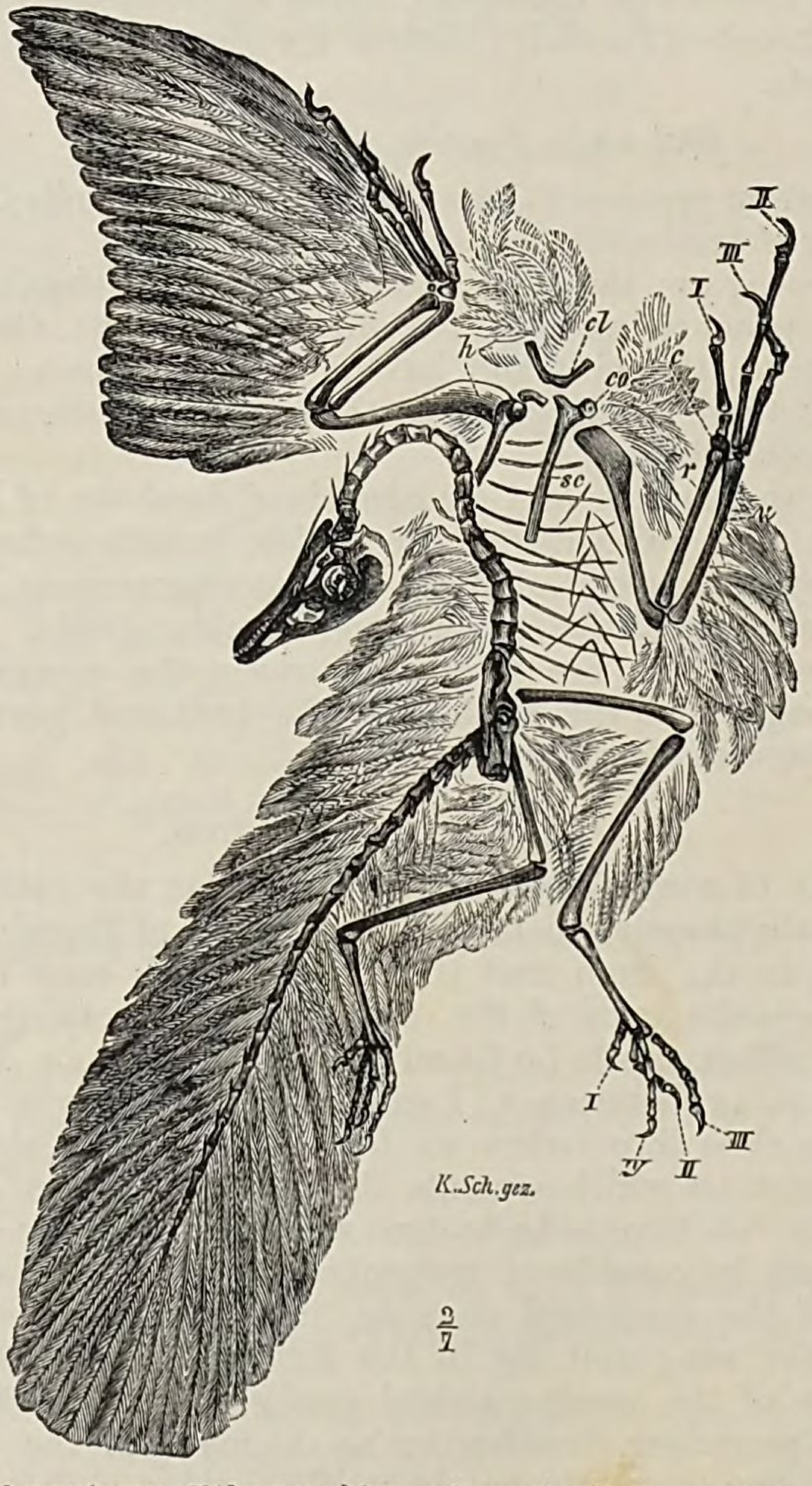


FIG. 996.—**Archæopteryx lithographica.** From the Berlin specimen. *c.* carpal; *cl.* furcula; *co.* coracoid; *h.* humerus; *r.* radius; *sc.* scapula; *u.* ulna; I—IV, digits.

Bavaria, belonging to the Upper Jurassic period. The Bird (Fig. 996) was about the size of a Crow, and in both fossils not only are the bones preserved, but also many of the feathers.

The most striking feature in the organization of the Bird is the fact that the *tail* is composed of about 18—20 free caudal vertebræ, gradually tapering to the distal end as in a Lizard. The *rectrices* are arranged in two rows, one on each side of the caudal vertebræ, producing a long tail quite unlike that of any existing Bird. The centra probably had flat faces. In addition to cervical and thoracic ribs there were *abdominal ribs*, like those of Hatteria and Crocodiles.

The skull (Fig. 997) is proportionately large, with rounded brain-case and strong jaws, in each of which is a series of conical *teeth*.

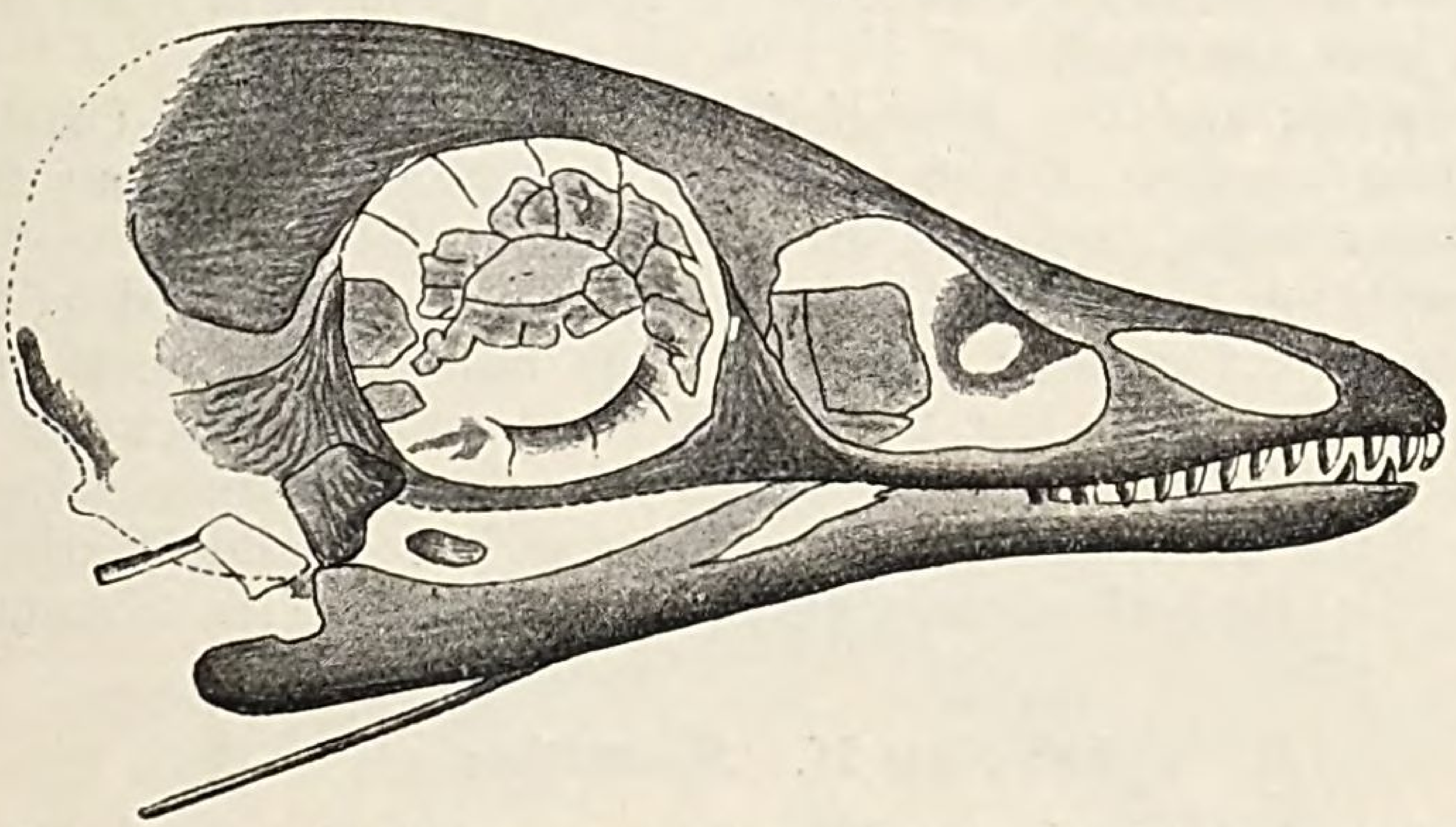


FIG. 997.—**Archæopteryx lithographica.** The Skull, showing teeth and sclerotic plates. (From Headley, after Dames.)

There is no trace of sternum in either specimen, and the coracoids (*co.*) are only partially visible: the scapulæ (*sc.*) are slender, curved bones, and there is a U-shaped furcula (*cl.*).

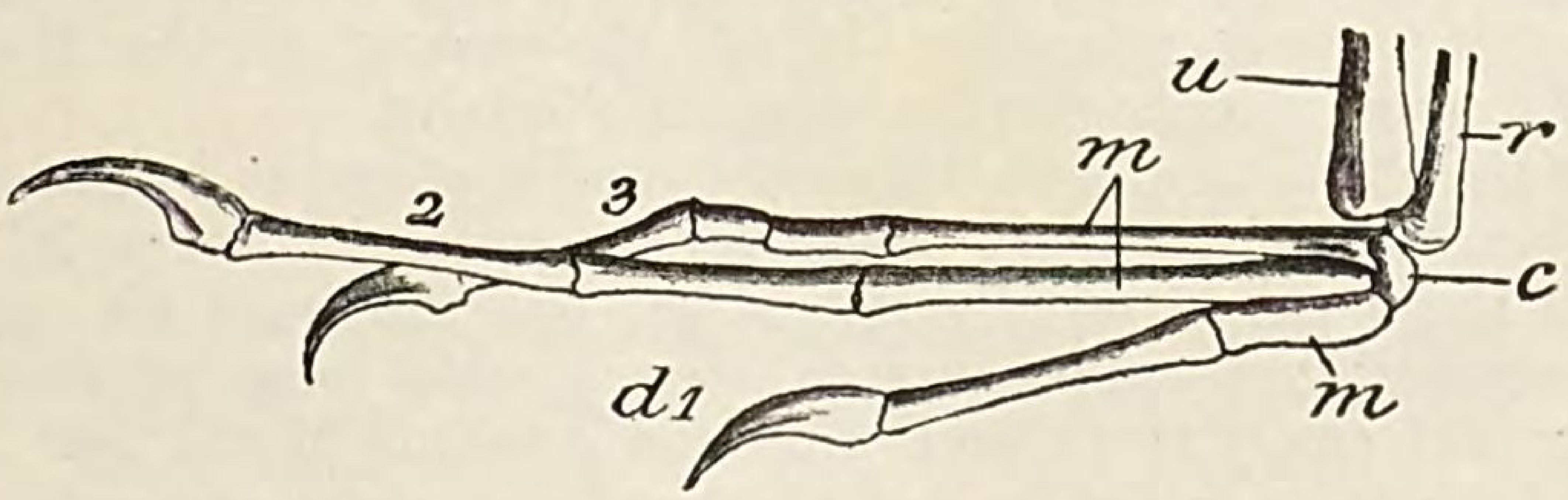


FIG. 998.—**Archæopteryx lithographica.** The left manus. *c.* carpal; *d. 1*, first digit; *m. m.* metacarpals; *r.* radius; *u.* ulna; *2*, second digit; *3*, third digit. (From Headley, after Dames.)

The bones of the upper and fore-arm are of the normal avian character: only one carpal is certainly known (Fig. 998, *c.*): it apparently belongs to the distal row, and is closely applied

to, and may perhaps have been ankylosed with the first and second metacarpals. Three digits (*d. 1, 2, 3*) are clearly visible in the more perfect of the two specimens—that in the Berlin Museum—the metacarpals of which are usually stated to be all free, in which case there is no carpo-metacarpus as in other Birds, and the hand approaches the normal reptilian type. Doubt has, however, recently been thrown on this statement. The number of phalanges follows the usual reptilian rule, two to the first digit, three to the second, and four to the third, and the ungual phalanx of all three digits is claw-shaped, and doubtless supported a horny claw.

The *remiges*, like the rectrices, are in a wonderful state of preservation (Fig. 996), and are divisible, as usual, into primaries or metacarpo-digitals and secondaries or cubitals. The primaries were probably attached to the second or to the second and third of the digits just described.

The *pelvis* and the *hind-limb* have the usual avian character. The foot consists of a slender tarso-metatarsus and four digits, the hallux being small and directed backwards.

In addition to the wing and tail-quills already referred to, there are remains of contour feathers at the base of the neck and of wing-coverts. Moreover, the rectrices are continued forwards by a series of large feathers, which extend for some distance along the sides of the body, and a row of similar but smaller feathers is attached along both anterior and posterior faces of the tibio-tarsus.

Sub-Class II.—Neornithes

External Characters.—In the general build of the body the Neornithes differ from Archaeopteryx chiefly in the shorter and stouter trunk, and in the point of articulation of the hind-limbs being thrown forward, so as to be almost directly below the centre of gravity of the body: the animal is thus enabled without effort to support itself on the legs alone. In a word Birds are essentially bipedal, the only exception being the young of the Hoatzin (*Opisthocomus*), which uses its wings in climbing.

The neck is always well developed, and is often, as in the Swan and Flamingo, of immense proportional length. The cranial portion of the head is usually not large, but the beak may attain extraordinary dimensions, and exhibits a wide range of form. It may be extremely short and wide for catching Moths and other flying Insects, as in Swifts and Goatsuckers; short and conical for eating fruit, as in Finches; strongly hooked for tearing the bodies of animals, as in Birds of Prey, or for rending fruits of various kinds, as in Parrots; long, conical, and of great strength, as in Storks; slender and elongated, as in Swifts, Ibises, and Curlews; broad and flattened for feeding in mud, as in Ducks and Geese; expanded at the end as in Spoonbills; immensely enlarged as in Hornbills and

Toucans. It is most commonly bent downwards at the tip, but may be straight or curved upwards, as in the Avocet, or bent to one side as in the New Zealand Crook-billed Plover. It is sometimes, as in the Toucans, brilliantly coloured, and there may also be bright coloration of the cere, as in the Macaws, and of naked spaces on the head, as in the Cassowaries. In the latter the head is produced into a great horny prominence or "casque," supported by an elevation of the roof of the skull. The cere is frequently absent. The nostrils are placed at the base of the beak except in Apteryx, in which they are at the tip.

The essential structure of the wing—apart from its feathers—is very uniform. As a rule all three digits are devoid of claws, as in the Pigeon, but the Ostrich has claws on all three digits; Rhea on the first and sometimes on the second and third; the Cassowary, Emu, and Kiwi (Fig. 999, B) on the second; the Crested Screamer (*Chauna*) and two other species, and, as a rare abnormality, the Common Fowl and Goose, on the first. With these exceptions, the hand of the adult bird has lost all the characters of a fore-foot; but in the young of the Hoatzin (*Opisthocomus*) claws are present on the first two digits (Fig. 999, A), which are

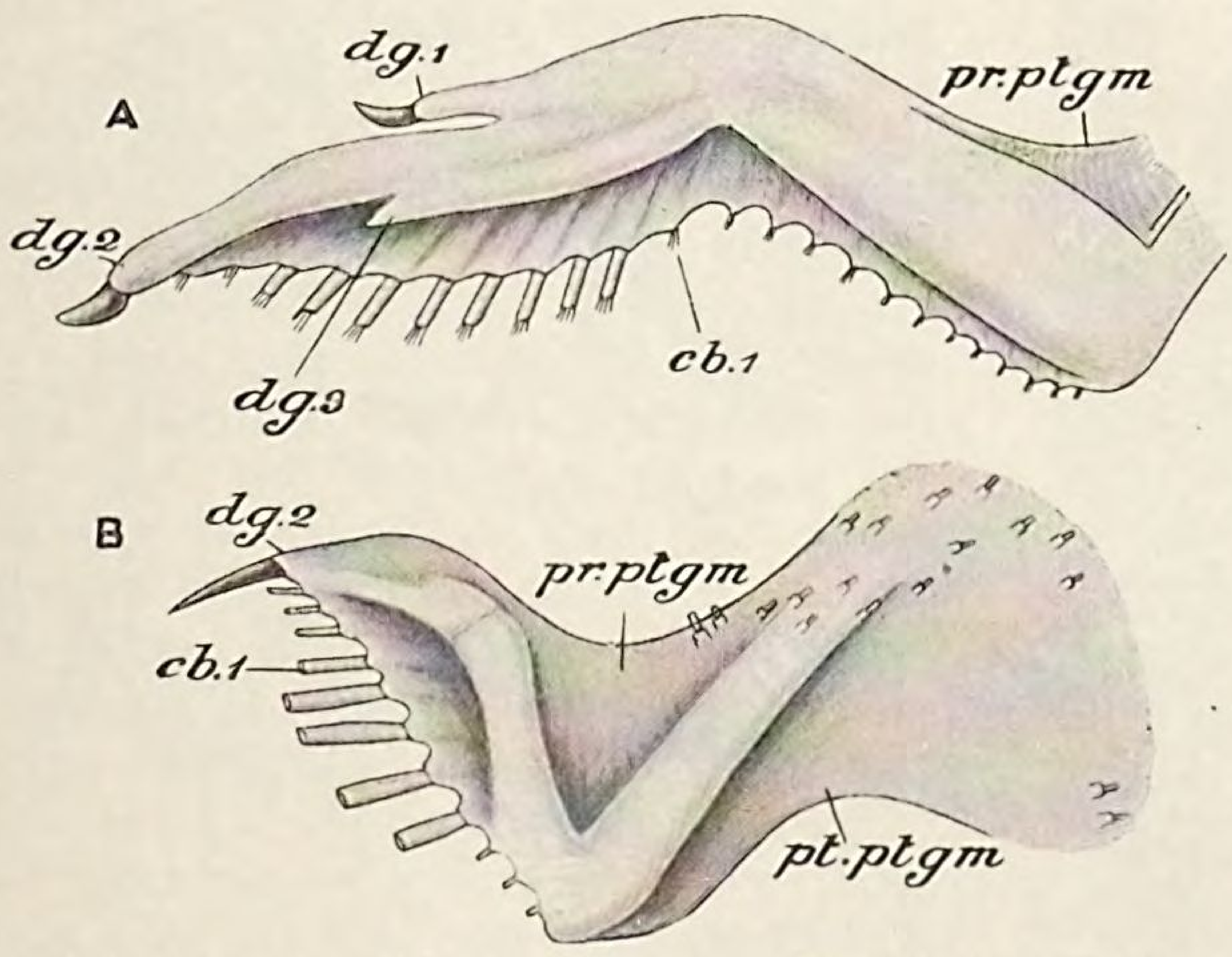


FIG. 999.—A, Wing of nestling of **Opisthocomus**; B, Wing of adult **Apteryx**; both from the inner (ventral) aspect. *cb. 1*, first cubital remex; *dg. 1*, *dg. 2*, *dg. 3*, digits; *pr. ptgm.* pre-patagium; *pt. ptgm.* post-patagium. (A, after Pycraft; B, after T. J. Parker.)

sufficiently mobile to be used in climbing. Besides the true claws horny *spurs* are sometimes present on the carpus and metacarpus.

There is almost every gradation in the proportional length of the hind-limb, from Birds in which nothing but the foot projects beyond the contour feathers, and even the toes may be feathered, to the long-legged Storks and Cranes, in which the distal

part of the tibio-tarsus is covered with scales as well as the foot. In aquatic forms a fold of skin or *web* is stretched between the toes, sometimes including all four digits, as in the Cormorants; sometimes leaving the hallux free, sometimes forming a separate fringe to each digit, as in the Coots and Grebes. As to the toes themselves, the commonest arrangement is for the hallux to be directed backwards, and Nos. 2, 3, and 4, forwards, but in the Owls No. 4 is reversible, *i.e.*, can be turned in either direction, and in the Parrots, Woodpeckers, &c., it, as well as the hallux, is permanently turned backwards. In the Swifts, on the other hand, all four toes turn forwards. The hallux is frequently vestigial or absent, and in the Ostrich No. 4 has also atrophied, producing the characteristic two-toed foot of that Bird.

Pterylosis.—With the exception of the Penguins, most Carinatæ have the feathers arranged in distinct feather-tracts or

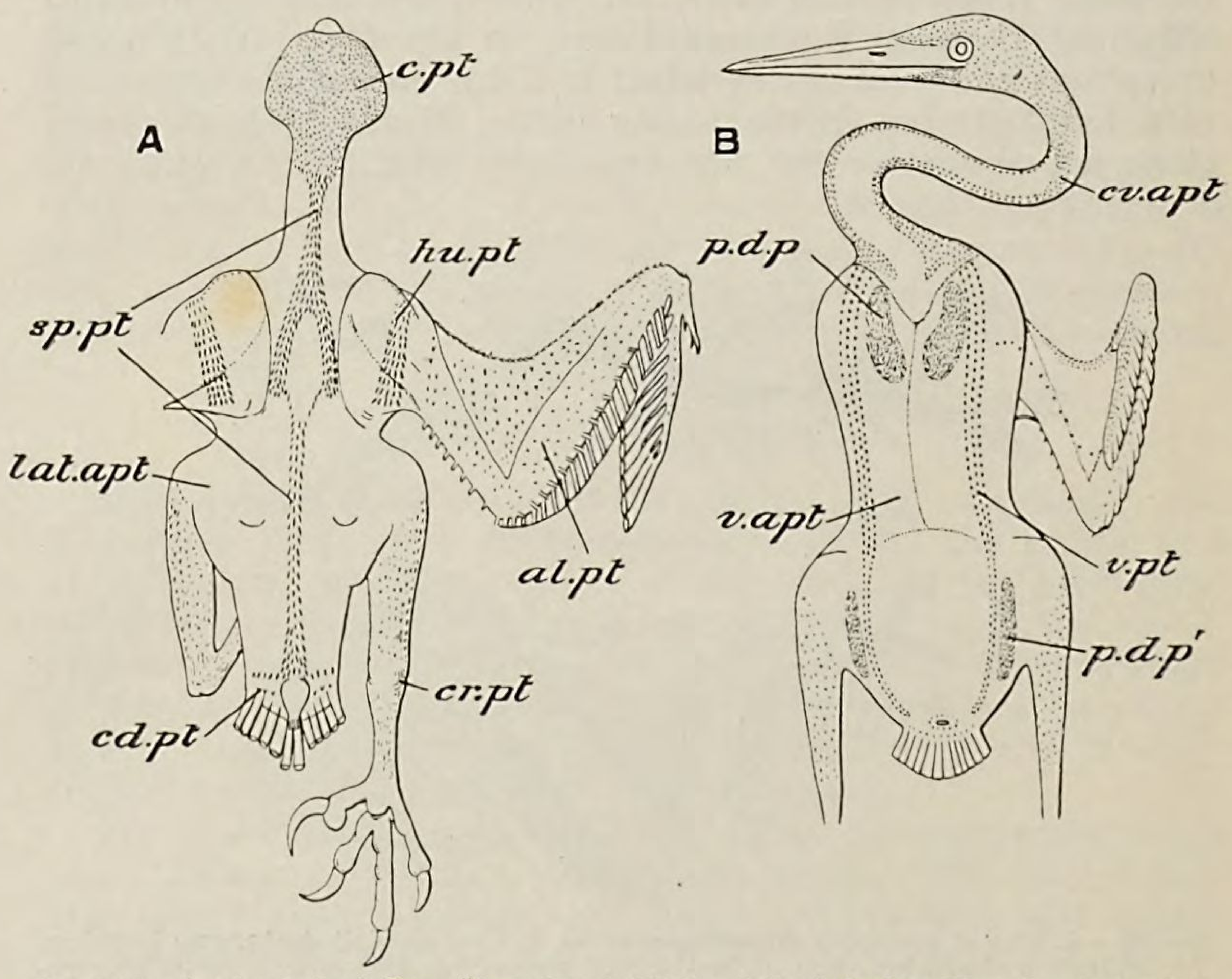


FIG. 1000.—A, pterylosis of **Gypaëtos** (Bearded Vulture), B, of **Ardea** (Heron). *al. pt*, wing-tract; *c. pt*, head-tract; *cr. pt*, crural tract; *cv. apt*. cervical space; *cd. pt*, caudal tract; *hu. pt*, humeral tract; *lat. apt*, lateral space; *p. d. p.*, *p. d. p'*. powder down patches; *sp. pt*, spinal tract; *v. apt*, ventral space; *v. pt*, ventral tract.

pterylæ, separated by apteria or featherless spaces. These are commonly much more distinct than in the Pigeon (Fig. 1000), and their form and arrangement and of importance in classification. In the Ratitæ, apteria are usually found only in the young, the adult

having a uniform covering of feathers. The Ratitæ, also, have nothing more than the merest trace of hooklets on the barbules, so that the barbs do not interlock and the vanes of the feathers are downy or hair-like. The same is said to be the case in Hesperornis. In the Penguins the wing-feathers are degenerate and scale-like.

Many Birds are quite naked when hatched, but in most cases the body is more or less completely covered by a temporary crop of feathers, the *nestling-downs,* of various forms, but always having a short axis, soft loose barbs, devoid of interlocking apparatus, and, except in the Emu, having no after-shaft (*vide infra*). They are succeeded, as already described, by the permanent feathers.

Many Birds, such as the Swan, possess *down-feathers* or *plumulæ* throughout life, interspersed among and hidden by the contour feathers or *pennæ,* In the Heron and some other Carinatæ are found *powder-down patches* (Fig. 1000, B, *p. d. p, p. d. p'*), areas of downs, the ends of which break off and make a fine dust. *Semi-plumes* are downs with a well-developed axis: *filoplumes,* as we have seen (Fig. 994, B), have an elongated axis and vestigial vexillum.

In many Birds there springs from the under side of the quill, near the superior umbilicus, a second vane, the *after-shaft* (Fig. 1001), usually smaller than the main shaft, but sometimes of equal size. Both among Carinatæ and Ratitæ we find genera with double-shafted feathers and allied forms in which the after-shaft is rudimentary or absent.

The feathers are always shed or "moulted" at regular intervals, as a rule annually. The old feathers drop out and new ones are formed from the same pulps.



FIG. 1001.—**Casuarius** (Cassowary). Feather, showing after-shaft and disconnected barbs. (From Headley.)

The *colours* of feathers present great variety. Black, brown, red, orange, and yellow colours are due to the presence of definite pigments, *i.e.* are absorption-colours. White, and in some cases yellow, is produced by the total reflection of light from the spongy, air-containing substance of the feather, there being, as in nearly all other natural objects, no such thing as a white pigment. Blue, violet,

and in some cases green, are produced by the light from a brown pigment becoming broken up as it passes through the superficial layer of the feathers, in its passage to the eye: no blue or violet pigments occur in feathers, and green pigments are very rare. The beautiful metallic tints of many birds are entirely the result of structure, owing their existence to a thin, transparent, superficial layer, which acts as a prism: in such feathers the colour changes according to the relative position of the Bird and of the eye of the observer with regard to the source of light.

There is also infinite variety in the general coloration of Birds. In many the colouring is distinctly protective, harmonising with the environment, and even changing with the latter, as in the Ptarmigan, which is greyish-brown in summer, white in winter, the former hue helping to conceal the Bird among herbage, the latter on snow. Frequently, as in Pheasants and Birds of Paradise, the female alone is protectively coloured, while the male presents the most varied and brilliant tints, enhanced by crests, plumes or tufts of feathers on the wings, elongated tail, &c. &c. These have been variously explained as "courtship colours" for attracting the female; as due simply to the exuberant vitality of the male Bird; or as helping to keep the number of males within proper limits by rendering them conspicuous to their enemies. Such ornaments as the bars and spots on the wings and tail of many gregarious birds, such as Plovers, fully exposed only during flight, and often widely different in closely allied species, have been explained as "recognition marks," serving to enable stragglers to distinguish between a flock of their own and of some other species.

Skeleton.—The vast majority of Birds have saddle-shaped or heterocœlous cervical and thoracic vertebræ, but the thoracic vertebræ are opisthocœlous in the Impennes (Penguins), the Gaviæ (Gulls), and the Limicolæ (Plovers, &c.), while in the Icthyornithes alone they are bi-concave. The spaces between adjacent centra are traversed by a meniscus with a suspensory ligament as in the Pigeon (p. 358). The number of vertebræ is very variable, especially in the cervical region, where it rises to twenty-five in the Swan and sinks to nine in some Song-birds. There is very commonly more or less fusion of the thoracic vertebræ, and the formation of a syn-sacrum by the concrescence of the posterior thoracic, lumbar, sacral, and anterior caudal vertebræ, is universal. The posterior cervical and anterior thoracic vertebræ commonly bear strong *hypapophyses* or inferior processes for the origin of the great flexor muscles of the neck. The number of true sacral vertebræ varies from one to five. A pygostyle formed by the fusion of more or fewer of the caudal vertebræ, is of general occurrence, but is small and insignificant in the Ratitæ.

The *ribs* are always double-headed, the sternal ribs are ossified, not merely calcified, and are united with the vertebral ribs by

synovial joints. Ossified uncinates are nearly always present, and usually become ankylosed to the vertebral ribs.

What may be considered as the normal type of *sternum* is a broad plate, concave dorsally from side to side, and produced ventrally into an antero-posterior keel which is ossified from a distinct centre (Fig. 1002, A, *os. 1*). The posterior edge of the bone is either entire (D) or presents, on each side of the keel, one or two more or less deep notches (A, B) or foramina (C). In the Ratitæ

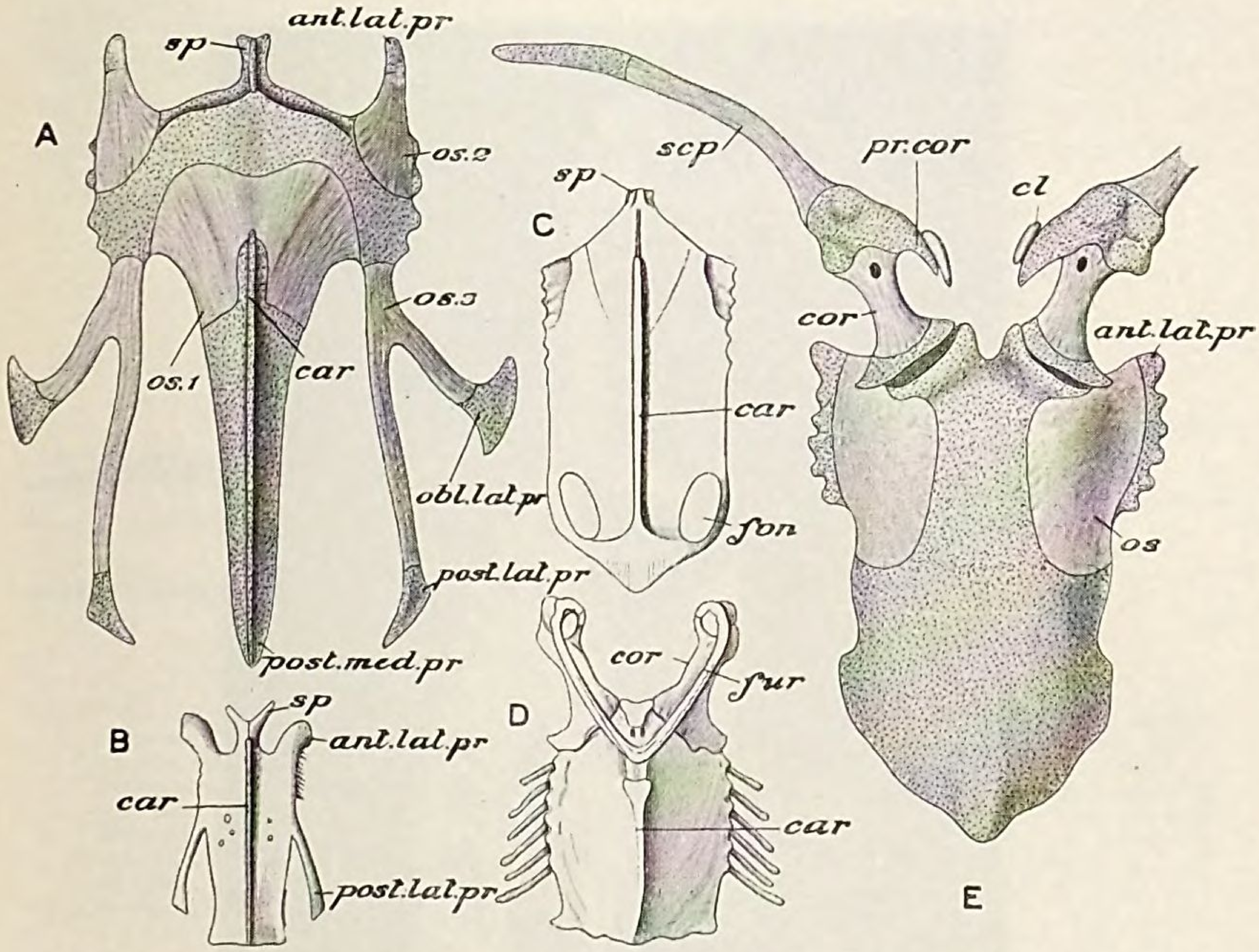


FIG. 1002.—Sterna of various Birds. A, **Gallus** (common Fowl, young); B, **Turdus** (Thrush); C, **Vultur** (Vulture); D, **Procellaria** (Petrel); E **Casuarius** (Cassowary). *ant. lat. pr.* anterior lateral process; *car.* carina; *cl.* clavicle; *cor.* coracoid; *fon.* fontanelle; *fur.* furcula; *obl. lat. pr.* oblique lateral process; *os.* paired ossification of sternum in E; *os. 1*, carinal ossification in A; *os. 2*, *os. 3.* lateral ossifications; *post. med. pr.* posterior median process; *post. lat. pr.* posterior lateral process; *pr. cor.* pro-coracoid; *scp.* scapula; *sp.* spina sterni. (A and E after W. K. Parker; B, C, and D, from Bronn's *Thierreich.*)

(E) the keel is either absent or reduced to the merest vestige, and there is no trace of the carinal ossification in the young. External to the coracoid grooves the anterior edge of the sternum is produced into larger or smaller antero-lateral processes (*ant. lat. pr.*): in the Emu these are of great size and are closely applied to the pericardium.

It was upon the characters of the raft-like sternum that the group Ratitæ was founded, but the difference between them and the Carinatæ in this respect is not absolute, the ratite condition

having been acquired by many Carinatæ which have lost the power of flight. The keel is very small in *Ocydromus, Notornis*, and *Aptornis*, three flightless Rails—the latter extinct—from New Zealand, and is practically absent in the Dodo (*Didus*) and Solitaire (*Pezophaps*), two gigantic extinct Pigeons from Mauritius and Rodriguez, in the Kakapo or Ground-parrot (*Stringops*) of New Zealand, in the extinct Giant-goose (*Cnemiornis*) from the same country, and in Hesperornis. The absence of the carina may

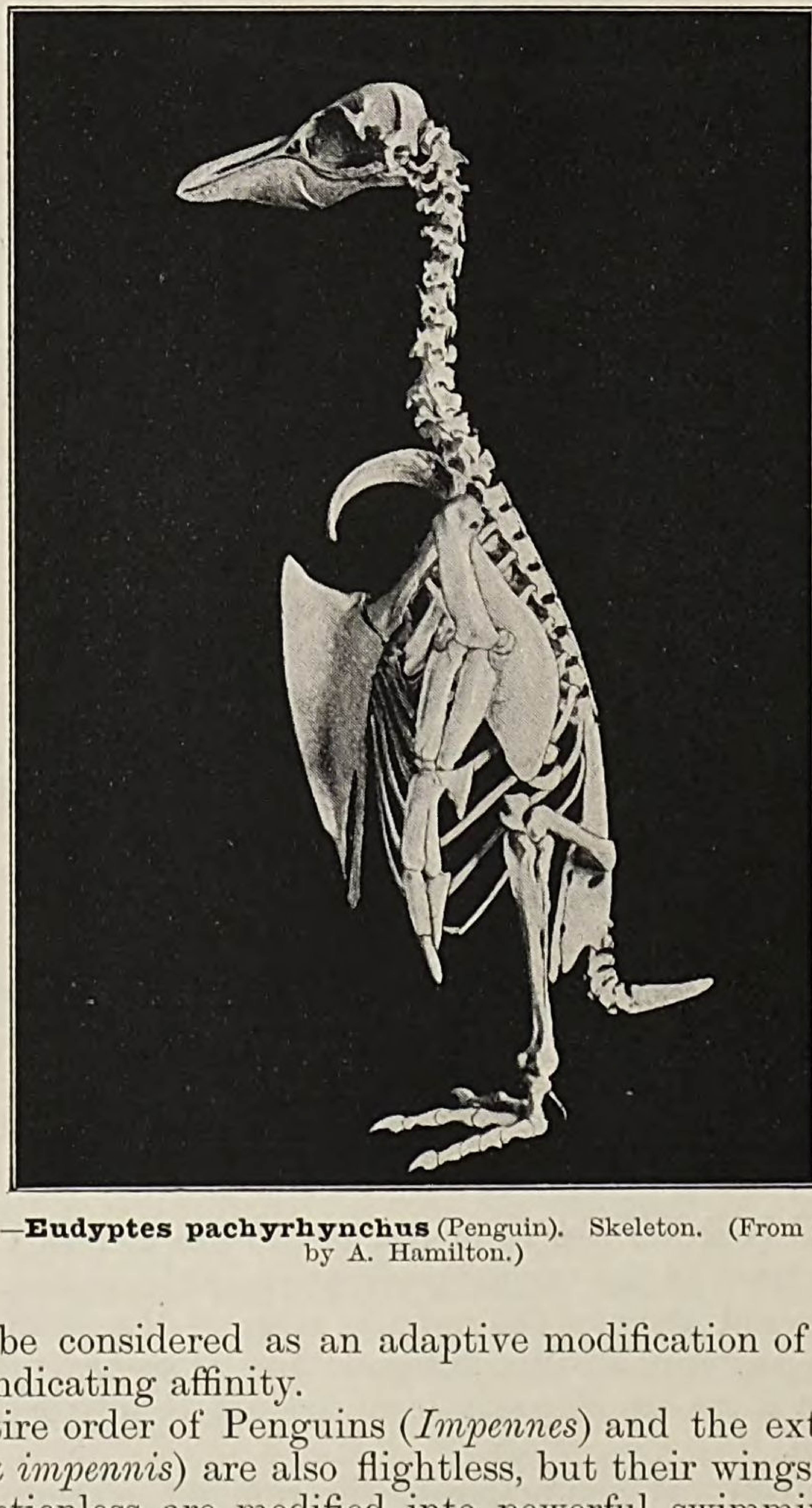


FIG. 1002 *is.*—**Eudyptes pachyrhynchus** (Penguin). Skeleton. (From a photograph by A. Hamilton.)

therefore be considered as an adaptive modification of no significance as indicating affinity.

The entire order of Penguins (*Impennes*) and the extinct Great Auk (*Alca impennis*) are also flightless, but their wings, instead of being functionless, are modified into powerful swimming paddles (Fig. 1002 *bis*). There has therefore, in these cases, been no reduction either of the pectoral muscles or of the carina.

The *skull* of Birds is generally remarkable for its huge orbits separated by a thin interorbital septum, and for the comparatively small size of the ethmoid bone and its turbinals. The most striking exception is afforded by the Kiwi (*Apteryx*) in which the orbits (Fig. 1003) are small and indistinct, while the olfactory chambers (*Ec. Eth*) extend backwards between the eyes; the orbits being therefore separated from one another by the whole width of the organ of smell. The same thing occurs, to a less degree, in the Moas.

In its essential features the skull is remarkably uniform throughout the class. The rounded form of the brain-case, more or less concealed externally by ridges for the attachment of muscles: the upper beak composed mainly of a great triradiate

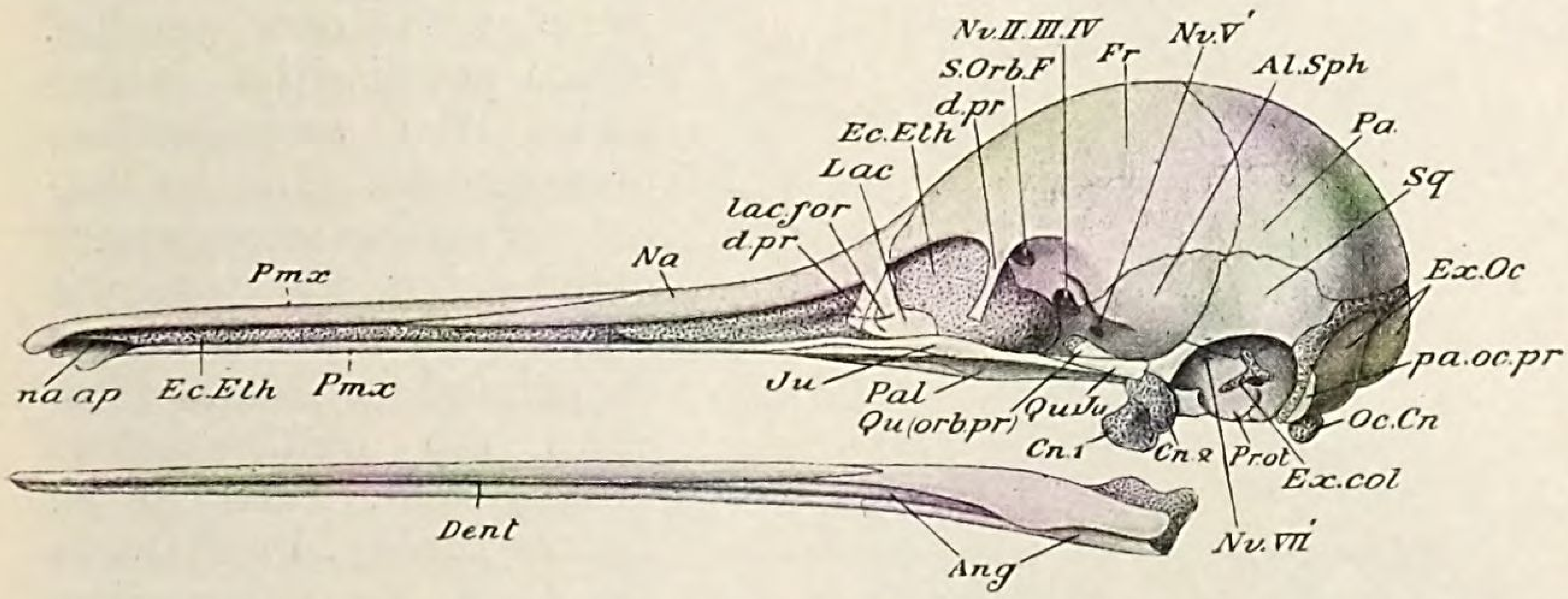


FIG. 1003.—**Apteryx mantelli.** Skull of a young specimen, side view. The cartilaginous parts are dotted. *Al.sph.* alisphenoid; *ang.* angular; *cn.* 1, *cn.* 2, condyle of quadrate; *Dent.* dentary; *d.pr.*, *d. pr.* descending processes of nasal and frontal; *Ec.Eth.* ecto-ethmoid; *Ex. Col.* extra-columella; *Ex. oc.* ex-occipital; *Ju* jugal; *Lac.* lacrymal; *lac. for.* lacrymal foramen; *Na.* nasal; *na. ap.* nasal aperture; *Nv. II, III, IV*, optic foramen, transmitting also the 3rd and 4th nerves; *Nv. V′*, foramen for orbito-nasal nerve; *Nv. VII.* for facial; *Pa.* parietal; *Pal.* palatine; *pa. oc. pr.* par-occipital process; *Pmx.* pre-maxilla; *Pr. ot.* pro-otic; *Qu. Ju.* quadrato-jugal; *Qu.* (*orb. pr.*) orbital process of quadrate; *S. orb. F.* supra-orbital foramen; *Sq.* squamosal. (After T. J. Parker.)

premaxilla; the single, small, rounded occipital condyle; the slender maxillo-jugal arch; the large parasphenoidal rostrum; the freely articulated quadrate, with its otic, orbital, and articular processes; the absence of the reptilian post-frontals; and the early ankylosis of the bones; all these characters are universal among Birds. There are, however, endless differences in detail, some of which, connected with the bones of the palate, are of importance in classification.

In the Ratitæ and the Tinamus (*Crypturi*) there are large basi-pterygoid processes (Fig. 1004, *B. ptg. pr*) springing, as in Lizards, from the basi-sphenoid, and articulating with the pterygoids near their posterior ends. The vomer (*Vo*) is large and broad, and is usually connected posteriorly with the palatines (*Pal*) which do not articulate with the rostrum. The maxillo-palatine

processes are comparatively small, and do not unite with one another or with the vomer. This arrangement of the bones of the palate is called *dromæognathous.*

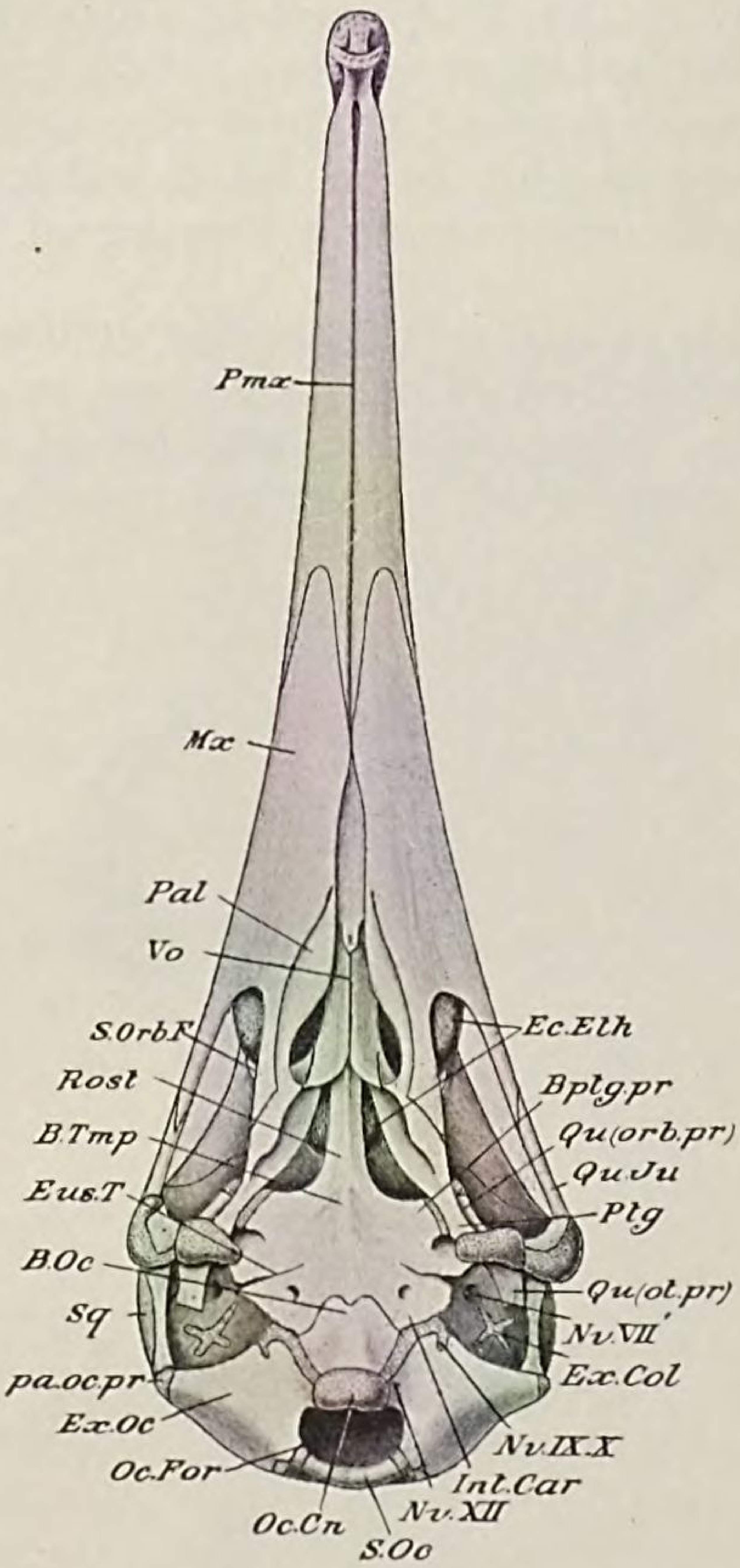


FIG. 1004.—**Apteryx mantelli.** Skull of young specimen, from below. The cartilaginous parts are dotted. *B. Oc.* basi-occipital; *B. ptg. pr.* basi-pterygoid process; *B. Tmp.* basi-temporal; *Ec. Eth.* ecto-ethmoid; *Eus. T.* Eustachian tube; *Ex. Col.* extra-columella; *Ex. oc.* ex-occipital; *Int. car.* carotid foramen; *Mx.* maxilla; *Nv. VII,* foramen for facial; *Nv. IX, X,* for glossopharyngeal and vagus; *Nv XII,* for hypoglossal; *Oc. cn.* occipital condyle; *Oc. for.* foramen magnum; *Pal.* palatine; *pa. oc. pr.* par-occipital process; *Pmx.* pre-maxilla; *Ptg.* pterygoid; *Qu.* (*orb. pr.*) orbital process of quadrate; *Qu.* (*ot. pr.*) otic process; *Rost.* rostrum; *S. Oc.* (supra-occipital); *S. orb. F.* supra-orbital foramen; *Sq.* squamosal; *Vo.* vomer. (After T. J. Parker.)

In many Carinatæ, *e.g.* the Pigeon and the Fowl, the basi-pterygoid processes are either absent or spring from the base of the rostrum. The vomer is small and pointed, or may be absent, and the palatines articulate posteriorly with the rostrum. The maxillo-palatines do not unite with one another. These peculiarities characterise the *schizognathous* arrangement. In the Passeres a similar arrangement obtains, but the vomer is broad and truncated instead of pointed in front. This gives the *ægithognathous* arrangement. Lastly in the Storks, Birds of Prey, Ducks and Geese, &c., the maxillo-palatines (Fig. 1005, *mx. p*) fuse with one another in the middle line, often giving rise to a flat, spongy palate and producing the *desmognathous* arrangement.

The most specialised form of skull is found in the Parrots (Fig. 1005 *bis*). In many Birds the nasals and the ascending process of the premaxilla are very thin and elastic where they join the skull, and there is an unossified space in the mesethmoid, so that the upper beak is capable of a considerable amount of movement in the vertical plane. In Parrots there is a true joint between the upper beak and the skull, allowing of that movement of the former which is so striking in the living

Bird. When the mandible is depressed the contraction of the digastric muscle causes a forward movement of the lower end of the quadrate, which pushes forwards the maxillo-jugal bar and the palatines and pterygoids, the latter sliding upon the rostrum. Both the maxillæ and the palatines are articulated in front with the premaxilla and together push it upwards; in this way depression of the lower, produces an automatic raising of the upper, jaw. The great size and strength of both premaxilla and mandible are remarkable, as also is the fact that the orbit is completely surrounded by bone, a backward process of the lacrymal being joined beneath it by a forward process of the frontal.

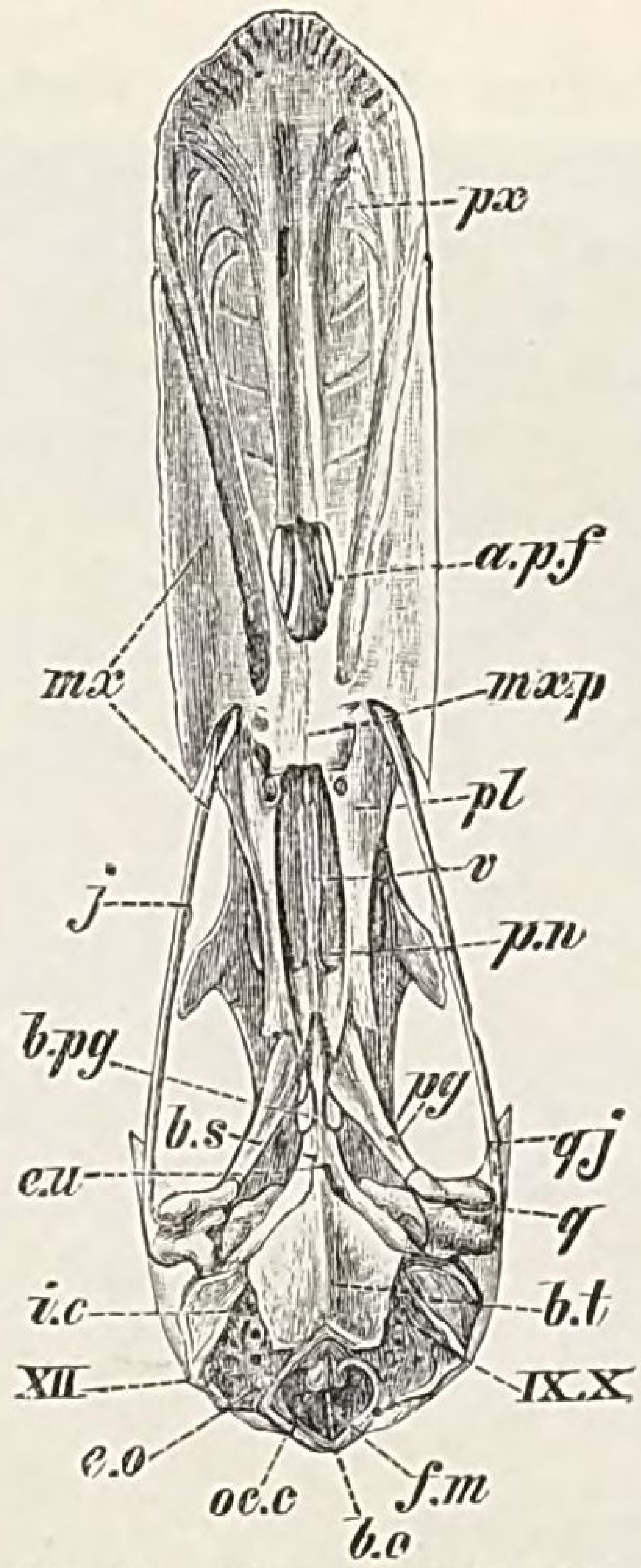


FIG. 1005.—**Anas boschas** (Duck). Ventral view of Skull. *a. p. f.* anterior palatine foramen; *b. o.* basi-occipital; *b. pg.* basi-pterygoid process; *b. s.* basi-sphenoid; *b. t.* basi-temporal; *e. o.* ex-occipital; *eu.* aperture of Eustachian tube; *f. m.* foramen magnum; *i. c.* internal carotid foramen; *j.* jugal; *mx.* maxilla; *mx. p.* maxillo-palatine process; *oc. c.* occipital condyle; *pl.* palatine; *p. n.* posterior nares; *px.* pre-maxilla; *q.* quadrate; *q. j.* quadrato-jugal; *v.* vomer; *IX, X,* foramen for ninth and tenth nerves; *XII,* for twelfth nerve. (From Wiedersheim's *Vertebrata*.)

The *mandible* contains in the young Bird the six bones on each side characteristic of Reptiles; the coronary is, however, often absent. As a rule the head of the *quadrate* articulates with the roof of the tympanic cavity by a single facet in Ratitæ, by a double facet in Carinatæ. The *hyoid* always agrees in essential respects with that of the Pigeon; in the Woodpecker the posterior cornua are curved round the head and fixed to the skull in the neighbourhood of the right nostril, a very flexible and protrusible tongue being produced.

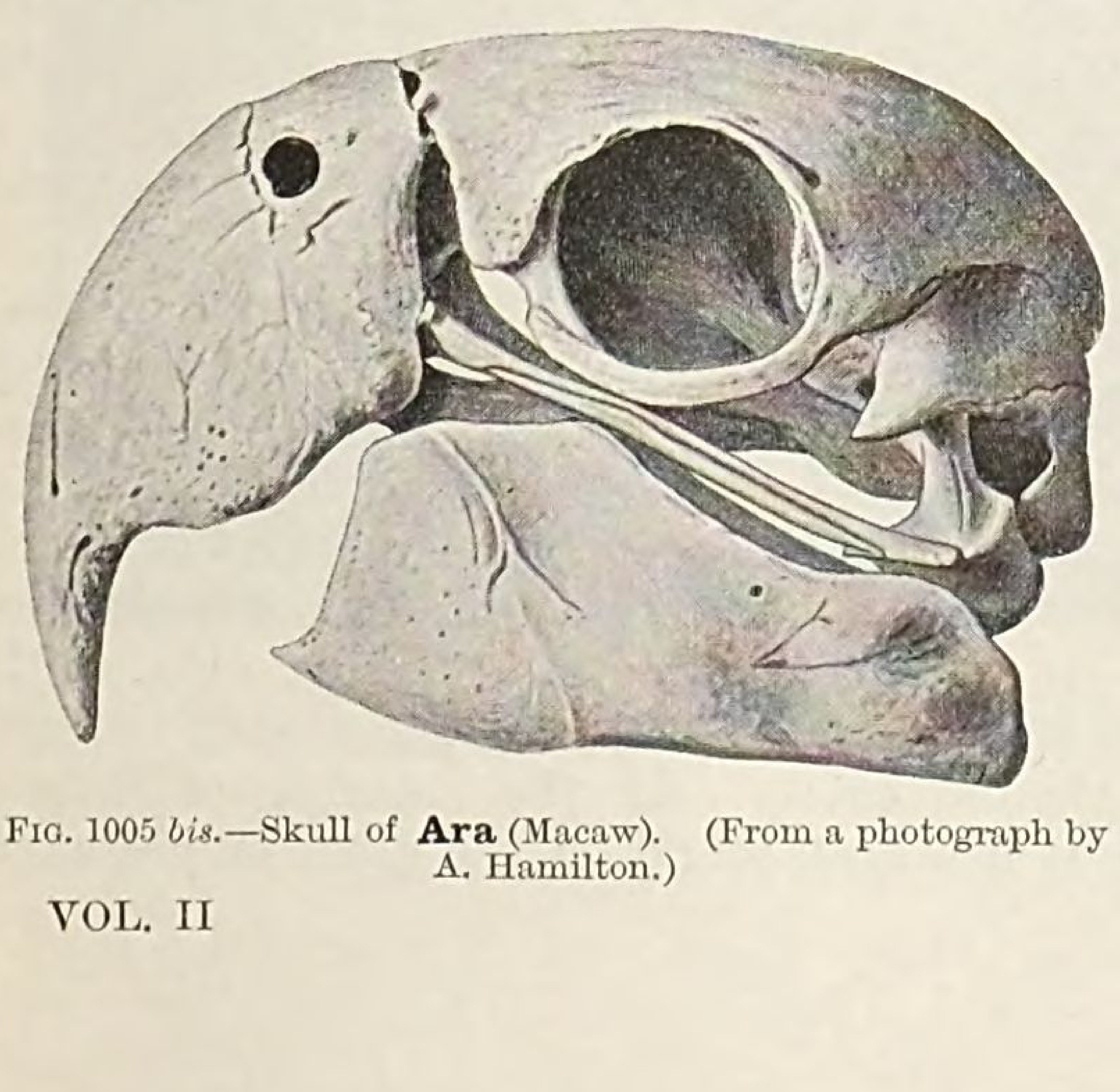


FIG. 1005 *bis*.—Skull of **Ara** (Macaw). (From a photograph by A. Hamilton.)

The structure of the *shoulder-girdle* furnishes one of the most fundamental distinctive

characters between Ratitæ and Carinatæ, but, as with the sternum, the differences are adaptive and not of phylogenetic significance. In most Carinatæ both coracoid and scapula are large and united with one another by ligament; the coracoid has an acrocoracoid and the scapula an acromian process; the coraco-scapular angle is acute; and there is a furcula. In the Ratitæ the coracoid (Fig. 1006, *cor.*) and scapula (*scp.*) are much reduced in proportional size and are ankylosed with one another; the acrocoracoid (*acr. cor.*) and acromion (*acr.*) processes are reduced or absent; the coraco-scapular angle approaches two right angles; and there is no furcula, although separate vestiges of clavicles are present in the Emu and Cassowary. In some of the Moas (*Pachyornis*, &c.) the shoulder-girdle is wholly absent. But, as in the case of the sternum, the distinction is not absolute. In Hesperornis, the Dodo, the Solitaire, Aptornis, Notornis, Ocydromus, and Cnemiornis the bones of the shoulder-girdle are proportionally small, the coraco-scapular angle exceeds 90°, and in some cases, such as certain Parrakeets and Owls, the furcula is feeble, or represented by paired vestiges, or absent. Curiously enough, considering that increase in the coraco-scapular angle is usually correlated with diminished powers of flight, it also slightly exceeds 90° in the Albatross and some of its allies.

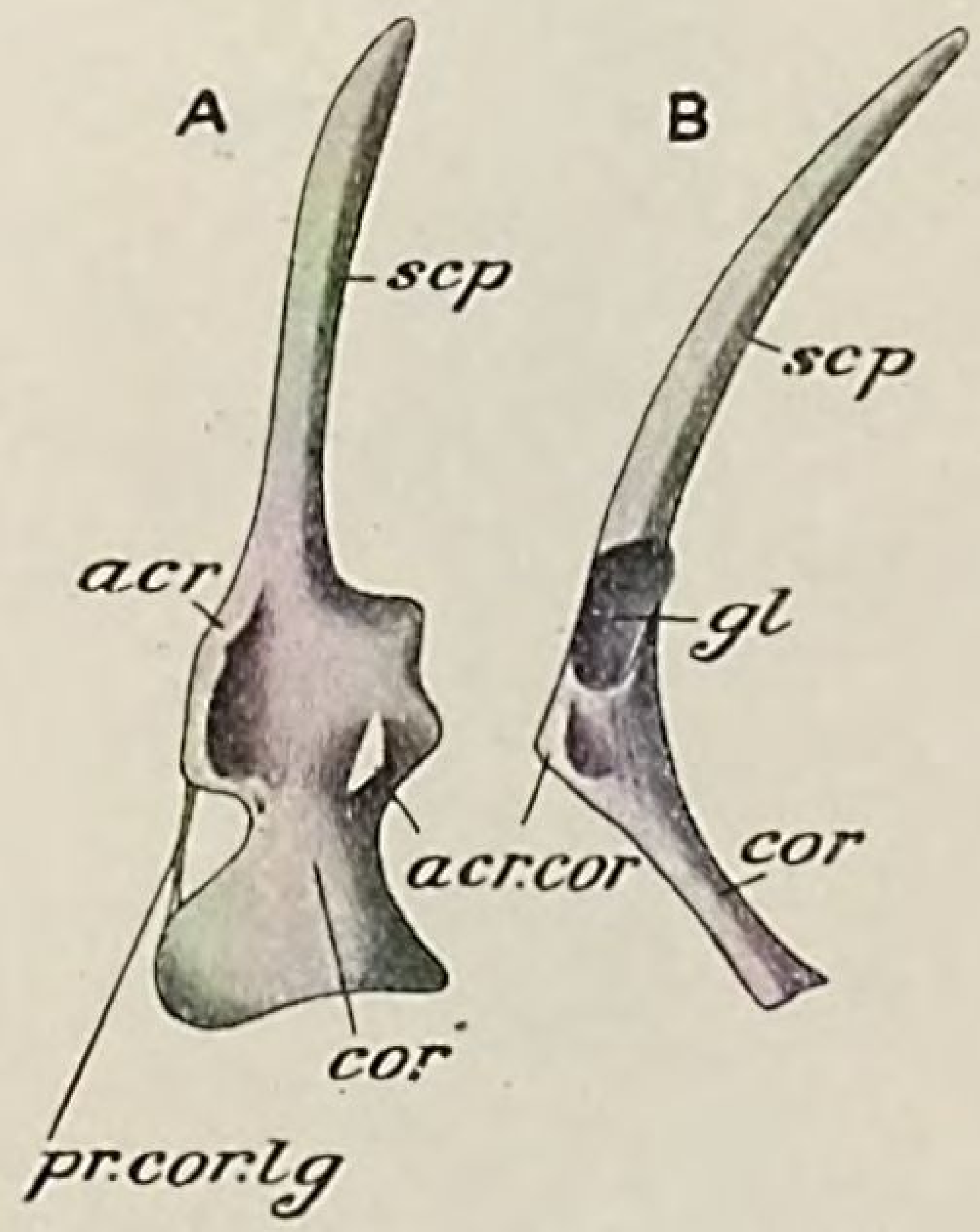


FIG. 1006.—**Apteryx mantelli.** The left shoulder-girdle. A, anterior; B, lateral (outer) surface. *acr.* acromion; *acr. cor.* acrocoracoid; *cor.* coracoid; *gl.* glenoid cavity; *pr. cor. lg.* pro-coracoid reduced to a ligament; *scp.* scapula. (After T. J. Parker.)

In most adult Birds the procoracoid is reduced to a process on the dorsal end of the coracoid, but in the Ostrich and in the embryo of Apteryx it is well developed and separated by a fenestra from the coracoid. A small bone, the *accessory scapula*, is sometimes found on the outer side of the shoulder joint.

The variations in the structure of the wing are mostly matters of proportion, but a remarkable flattening of all the bones is very characteristic of Penguins (Fig. 1002 *bis*), which are further distinguished by the presence of a sesamoid bone, the *patella ulnaris*, taking the place of the olecranon process. In the Emu and Kiwi the first and third digits of the normal wing have atrophied during development, the middle one alone remaining. In the Moas (Fig. 1007) no trace of a wing has been found, and in one species only is there even a trace of the glenoid cavity. In the embryos of several Birds an additional digit has been found on the ulnar or postaxial

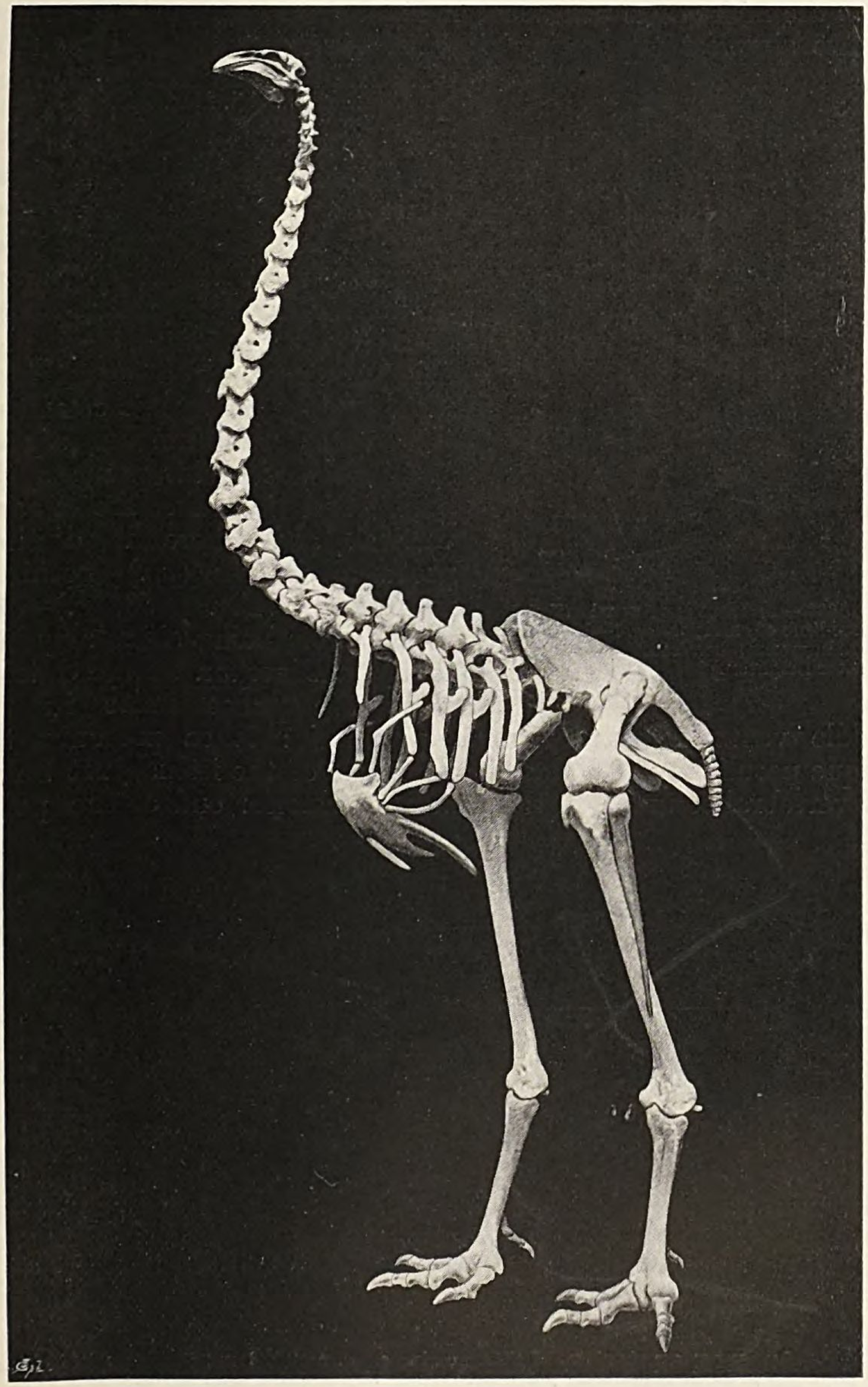


FIG. 1007.—Skeleton of **Dinornis robustus**, one of the Moas: actual height 9 ft. 6 in. (From a specimen at the Royal College of Surgeons, London.)

side (Fig. 1008, *dg. 4*): this brings the total number of digits up to four, the fifth of the pentadactyle hand alone being unrepresented.

The simplest type of *pelvic girdle* is found in Apteryx (Fig. 1009) and the Tinamus, in which both pubis and ischium are free along their whole length, as in Dinosaurs. In the Emu and Cassowary the pubis and ischium unite by cartilage or bone at their posterior end with the ilium, and in most Birds this union is extensive, the deep ischiatic notch being replaced by a small foramen. In the embryonic condition (Fig. 1010) the ilium has a very small pre-acetabular portion, the pubis and ischium are nearly vertical, and there is distinct pectineal process (*pp.*)—retained in Apteryx (Fig. 1009, *p.*)—the whole pubis being singularly like that of a Dinosaur. In the Ostrich alone the pubes unite in the middle ventral line to form a symphysis: Rhea presents the unique peculiarity of a dorsal symphysis of the ischia, just below the vertebral column: in the Emu the posterior end of the pubis

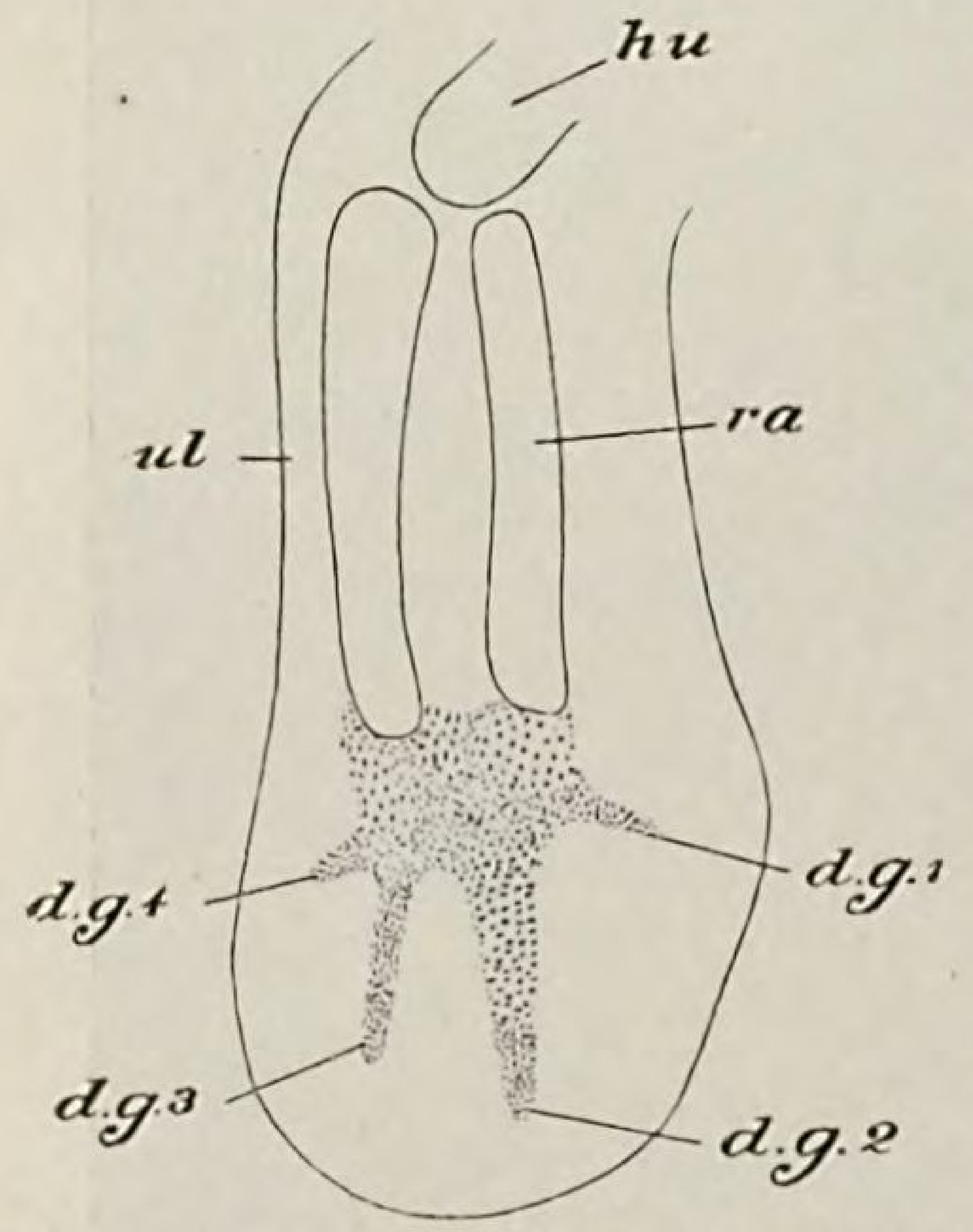


FIG. 1008.—**Sterna wilsoni** (Tern). Fore-limb of embryo. *dg.* 1—4, digits; *hu.* humerus; *ra.* radius; *ul.* ulna. (After Leighton.)

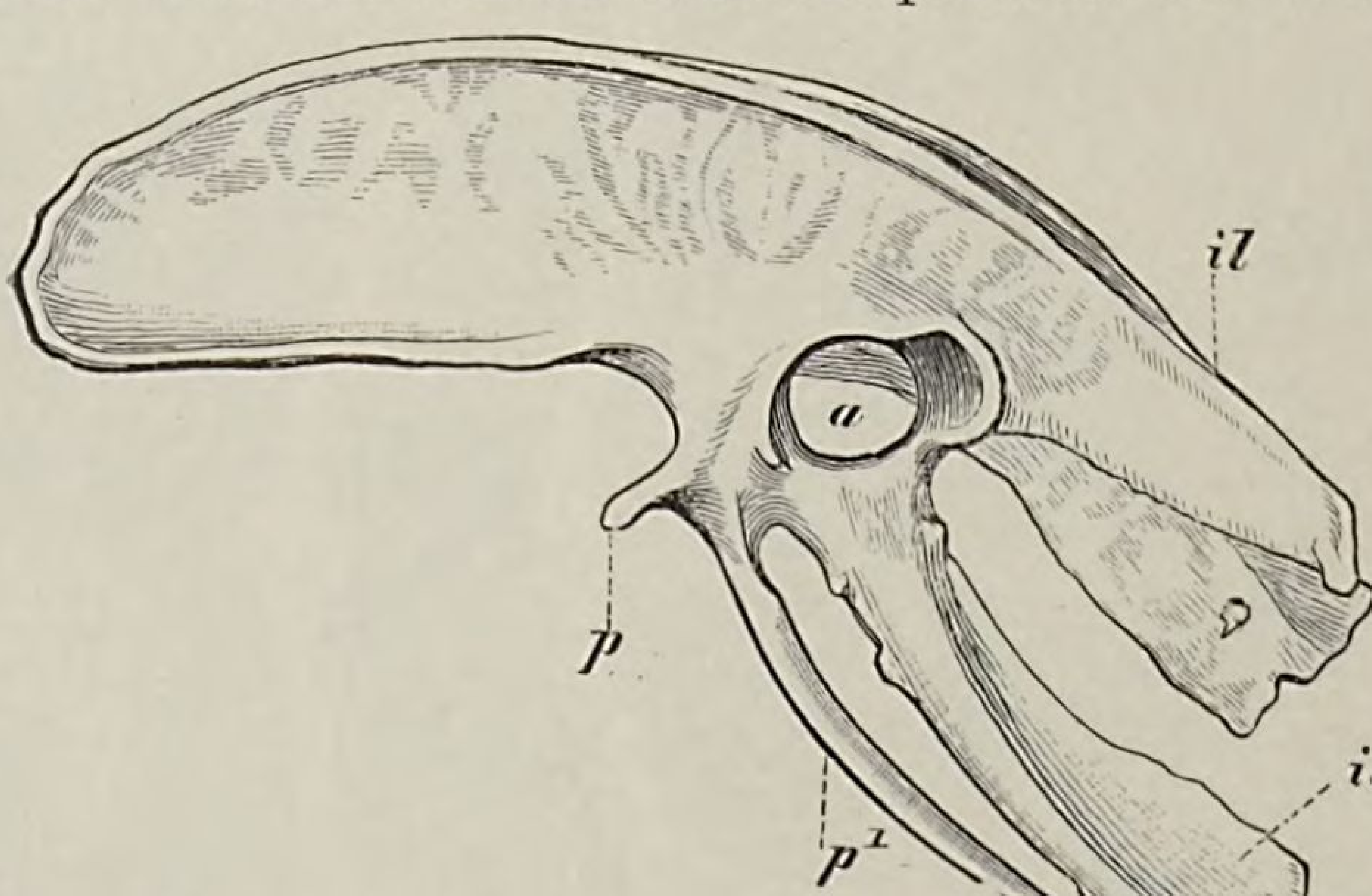


FIG. 1009.—**Apteryx australis.** Left innominate. *a.* acetabulum; *il.* ilium; *is.* ischium; *p.* pectineal process; p^1. pubis. (From Wiedersheim, after Marsh.)

gives off a slender process, which extends forwards close to the ventral edge of that bone and probably represents the *epi-pubis* of Reptiles.

The bones of the *hind-limb* are very uniform throughout the class, but the form of the tarso-metatarsus of Penguins is worthy of notice. It is short and wide, its three constituent metatarsals, though fused, are clearly distinguishable throughout their whole length, and the resemblance to the homologous part in Iguanodon is very striking. In the embryo (Fig. 1011) a vestige of the fifth digit (*mt. tsl. 5*) has been found in the form of a small rod of cartilage on the postaxial or fibular side. One or two free centralia may occur in the mesotarsal joint (Fig. 1007).

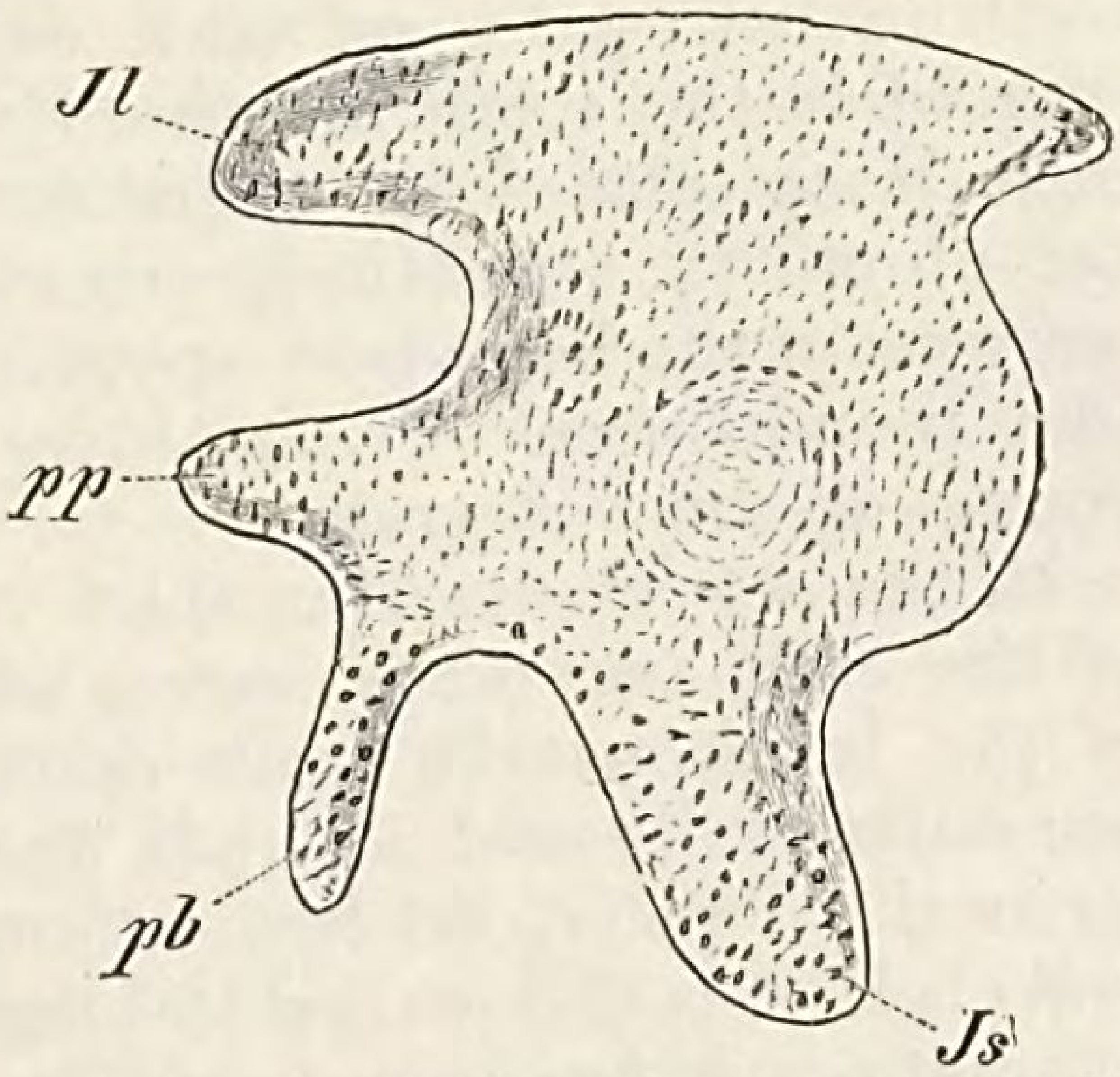


FIG. 1010.—**Gallus bankiva** (common Fowl). Innominate of a six days' embryo. *Il.* ilium ; *Is.* ischium ; *pb.* pubis ; *pp.* pectineal process. (From Wiedersheim, after Johnson.)

The skeleton is always more or less pneumatic, but there is no definite relation between pneumaticity and power of flight. A very usual arrangement is for all the bones to contain air except those of the fore-arm and hand, shank and foot. But in Apteryx, Penguins, and some Song-birds the skull alone is pneumatic, while in the Hornbill every bone in the body contains air.

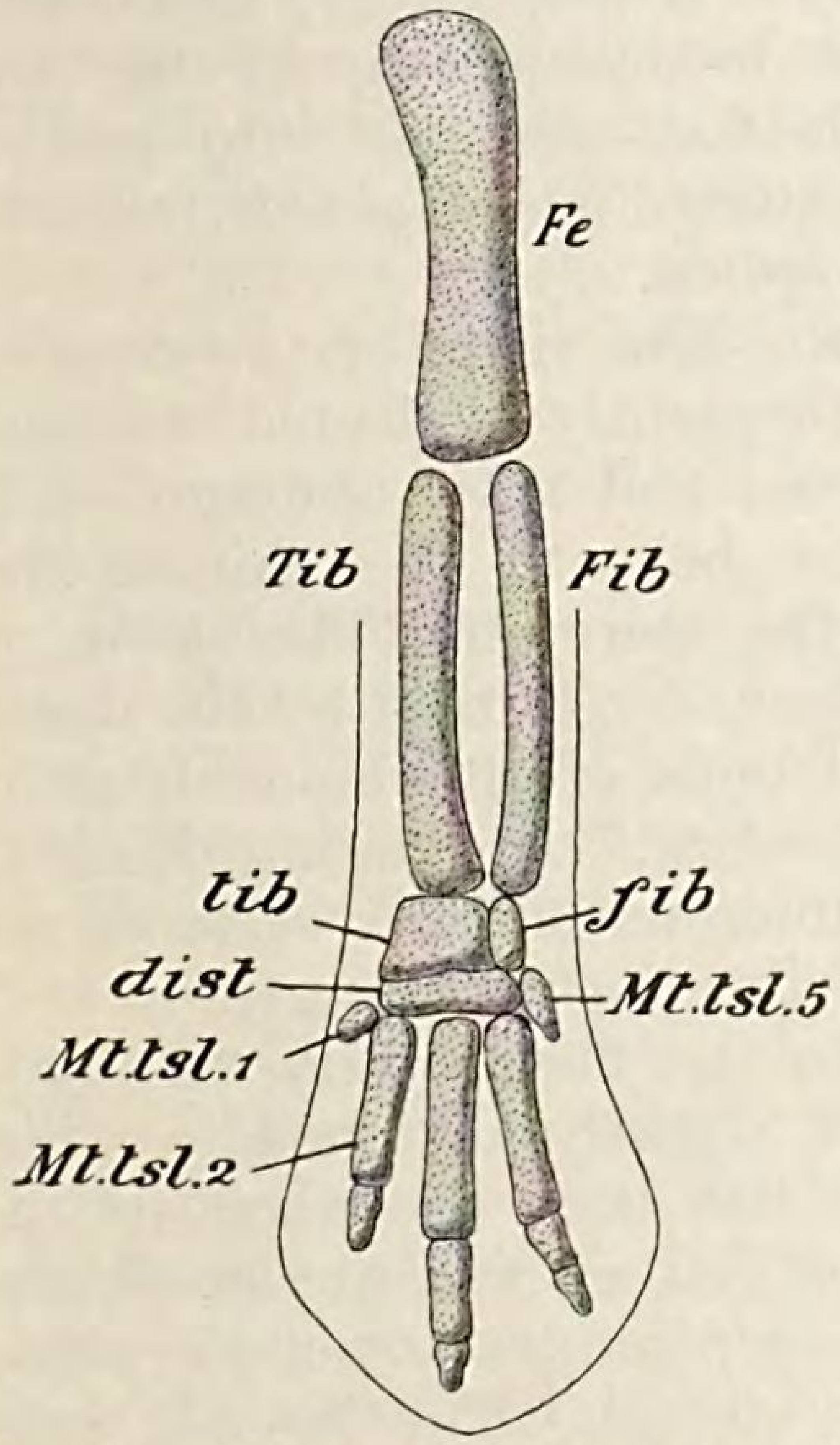


FIG. 1011.—**Apteryx oweni.** Left hind-limb of embryo, dorsal aspect. *dist.* distale ; *fe.* femur ; *Fib.* fibula ; *fib.* fibulare ; *Mt. tsl.1—5*, metatarsals ; *Tib.* tibia ; *tib.* tibiale. (After T. J. Parker.)

Myology.—As might be inferred from a study of the skeleton, the muscles of flight undergo a great reduction, often amounting to complete atrophy, in the Ratitæ, and to a less degree in the flightless Carinatæ. The presence or absence of an ambiens and of certain other muscles in the leg and in the wing furnish characters of considerable classificatory importance.

Digestive Organs.—In all existing Neornithes the jaws are covered by a horny beak and there are no *teeth*. But that teeth were present in the more primitive Birds, and have gradually been lost during the evolution of the

recent orders, seems certain from the fact that the cretaceous Birds were toothed. In Hesperornis (Fig. 993) there are long conical teeth in both jaws, set in a continuous groove. In Ichthyornis (Fig. 994) the teeth are thecodont, like those in the Crocodile, each being placed in a distinct socket. In Gastornis and in Odontopteryx, an extinct carinate form allied to the Anseres, the margins of the bony jaws are produced into strong, pointed, tooth-like prominences. Vestigial teeth have been discovered in the young of some Parrots.

In the *enteric canal* the chief variations have to do with the size of the crop and of the cœca, in the gizzard, and in the coiling of the intestine. In grain-eating Birds the gizzard has thick muscular walls and is lined by a thickened horny epithelium, as in the Pigeon: in flesh-eaters, such as Gulls, Petrels, Hawks, and Owls, it is thin walled and lined with epithelium of the ordinary character. It has been found by experiment that the carnivorous gizzard of a Gull becomes thick-walled under the influence of a diet of grain while the converse change is produced by feeding a Pigeon with meat. In the Common Fowl and many other Birds the cœca are of great length. A *gall-bladder* is usually present: the *spleen* is always small. The *tongue* may be pointed, as in the Pigeon; very long and protrusible, as in Woodpeckers; short and thick, as in Parrots; or modified for honey-sucking by the tip being produced either into a brush-like organ or into paired sucking-tubes. There are variously situated *buccal glands*, to some of which the name *salivary* is often applied.

Respiratory and Vocal Organs.—The rings of the *trachea* are always ossified: the tube is frequently deflected to one side by the crop, as in the Pigeon, and may undergo such an increase in length as to extend beneath the skin of the abdomen, or even into the keel of the sternum. The *syrinx* is either *tracheo-bronchial*, as in the Pigeon, *i.e.*, formed by the distal end of the trachea and the proximal ends of the bronchi, or is exclusively *tracheal* or exclusively *bronchial*. In singing Birds it is complex, and is provided with numerous muscles—five or six pairs—for altering the tension of the vibrating membrane.

The *lungs* are always firmly fixed to the dorsal body-wall by a pulmonary aponeurosis, and are but slightly distensible. The general arrangement of the air sacs has been described in the Pigeon (p. 371): in Apteryx the abdominal air sacs are small, and are completely enclosed by the oblique septum, so as not to extend into the abdominal cavity among the viscera. The bronchi send off branches at right angles.

The **Circulatory Organs** agree in all essential respects with those of the Pigeon: their most characteristic features are the large size of the heart, the muscular right auriculo-ventricular valve, the atrophy of the left aortic arch, and the vestigial character

of the renal portal system. The red blood-corpuscles are always oval and nucleated.

Nervous System and Sense Organs.—The *brain* is also very uniform in structure, being characterised by its short rounded hemispheres, large folded cerebellum produced forwards to meet the hemispheres, and laterally placed optic lobes. In the embryo the optic lobes have the normal dorsal position, and the whole brain resembles that of a Reptile. In Apteryx, in correlation with the reduction of the eyes, the optic lobes are very small, and are situated on the under side of the brain. Above the anterior commissure is a small bundle of fibres which has been considered as the homologue of the *hippocampal commissure* of Mammals.

Apteryx is also distinguished by the high development of the olfactory chamber, which extends from the tip of the beak to the level of the optic foramina: the turbinals are large and complex, and there is a vestige of the cartilage of Jacobson's organ. The small eye differs from that of all other Birds in the absence of a pecten, although a vestige of that organ occurs in the embryo. The structure of the *auditory organ* is very uniform throughout the class.

Urinogenital Organs.—In these, also, the general agreement with the Pigeon is very close, the most characteristic feature being the more or less complete atrophy of the right ovary and oviduct. The Megistanes, Rheæ, Anseres, and some other Birds have a penis in the form of a thickening of the ventral wall of the cloaca: it has a groove on the dorsal surface acting as a sperm-channel, and its distal end is invaginated, in the position of rest, by an elastic ligament. In the Ostrich there is a solid penis, like that of Chelonia and Crocodiles: it can be retracted into a pouch of the cloaca.

Development.—The process of development in Birds has been most thoroughly worked out in the Common Fowl, but enough is known of the embryology of other Birds to show that the differences are comparatively unimportant.

The *ovum* is always large owing to the great quantity of food-yolk: the protoplasm forms a small *germinal disc* at one pole. Impregnation is internal, and, as the oosperm passes down the oviduct it is coated by successive secretions from the oviducal glands. It first receives a coat of thick, viscid *albumen* (Fig. 1012, *alb.*), which, as the egg rotates during its passage, becomes coiled at either end into a twisted cord, the *chalaza* (*ch.*). Next, more fluid albumen (*alb.'*) is deposited layer by layer, then a tough, parchment-like *shell-membrane* (*sh. m.*), and finally a calcareous *shell* (*sh.*). The shell-membrane is double, and, at the broad end of the egg, the two layers are separate and enclose an air-cavity (*a.*). The shell may be white or variously coloured by special pigments: it consists of three layers, and is traversed by vertical pore-canals, which are

unbranched in the Carinatæ and in Apteryx, branched in the other Ratitæ.

The eggs may be laid on the bare ground or on the rocks by the sea-shore, as in Penguins and Auks, or on the ledges on inaccessible cliffs, as in the Sooty Albatross (*Diomedea fuliginosa*); but as a rule a *nest* is constructed for their reception by the parent Birds. This may be simply a hole in the sand, as in the Ostrich; a mere clearing on the hill-side surrounded by a low wall of earth, as in the Wandering Albatross (*Diomedea exulans*); or a cylinder with excavated top, built of grass, earth, and manure, as in the Mollymawks (*Diomedea melanophrys*, etc.). It may take the form of a burrow, as in many Petrels, Kingfishers, and Sand-martins, or it

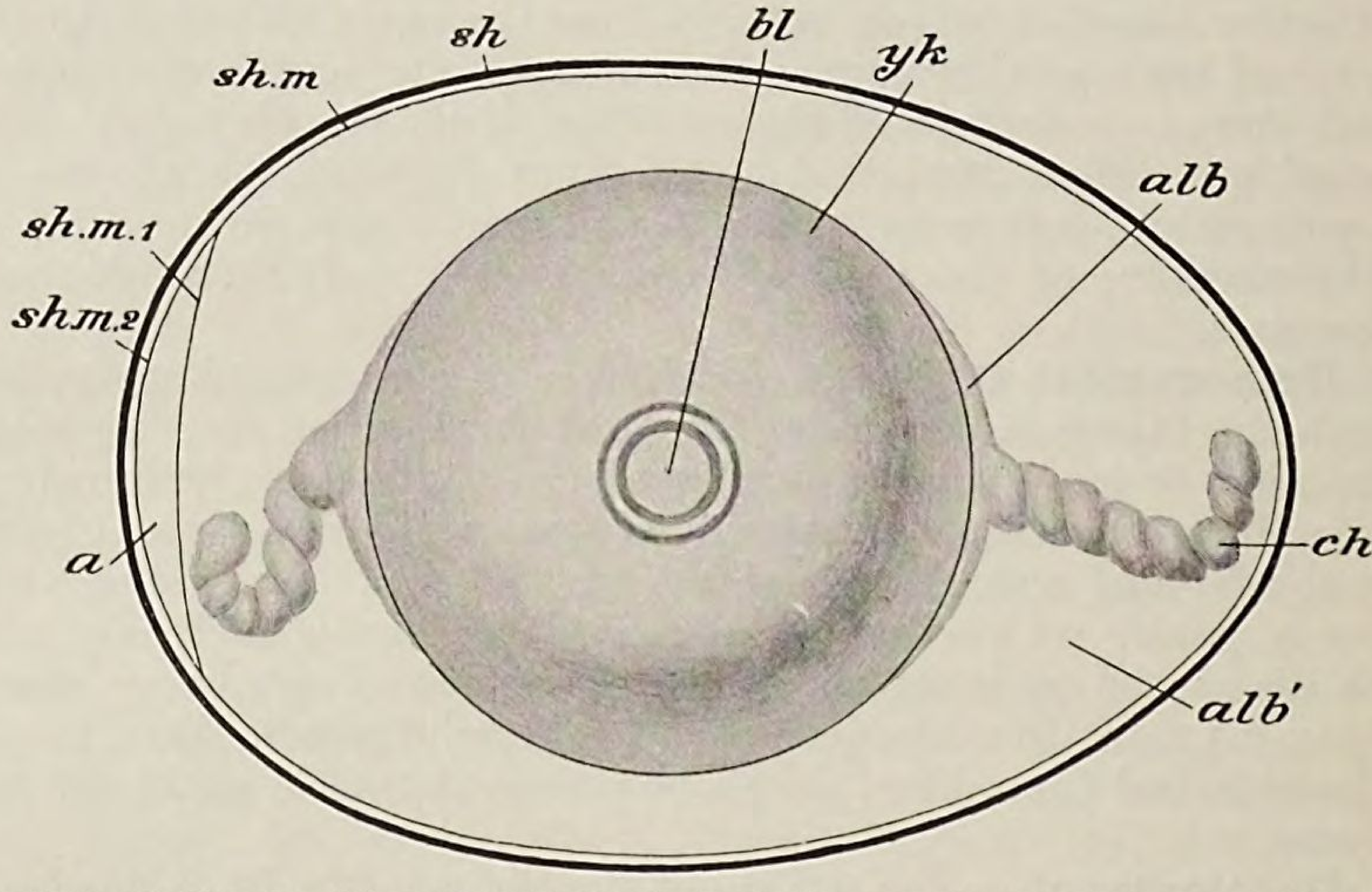


FIG. 1012.—**Gallus bankiva** (domestic Fowl). Semi-diagrammatic view of the egg at the time of hatching. *a.* air-space; *alb.* dense layer of albumen; *alb'.* more fluid albumen; *bl.* blastoderm; *ch.* chalaza; *sh.* shell; *sh. m.* shell-membrane; *sh. 1*, *sh. 2*, its two layers separated to enclose air-cavity. (From Marshall's *Embryology*, slightly altered.)

may be more or less elaborately built or woven of sticks, moss, leaves, hair, or feathers, showing every stage of constructive skill, from the rude contrivance of sticks of the Pigeon and Eagle, to the accurately constructed cup- or dome-shaped nests of many familiar Passeres. In the Tailor-Bird (*Orthotomus*) it is formed of leaves sewn together, the beak acting as needle: in a Malayan Swift (*Collocalia*) it is largely built of the secretion of the Bird's buccal glands.

The number of eggs laid varies from 15—18 in the Partridge, to a single one in many Sea-birds and in the Kiwi. As a rule the size of the eggs bears some proportion to that of the Bird, the smallest being those of Humming-birds, the largest those of the Moas and of Æpyornis: but in Apteryx the egg is of disproportionate size—

as large as a Swan's or an Albatross's, the Kiwi itself being no larger than a Barn-door Fowl.

Segmentation takes place during the passage of the egg down the oviduct, and results, as in Reptiles, in the formation of a *blastoderm* (Fig. 1012, *bl.*) occupying a small area at one pole of the yolk. After the egg is laid, the process of development is arrested unless the temperature is kept up to about 40° C.: this is usually done by the heat of the body of the parent Birds, one or both of which sit upon, or *incubate*, the eggs until the young are hatched; but in the Australian Mound-makers (*Megapodius*) the eggs are buried in heaps of decaying vegetable matter, the decomposition of which generates the necessary heat.

In the newly-laid egg the blastoderm is divisible into two parts, a central, clear *area pellucida* (Fig. 1013, *ar. pl.*) and a peripheral

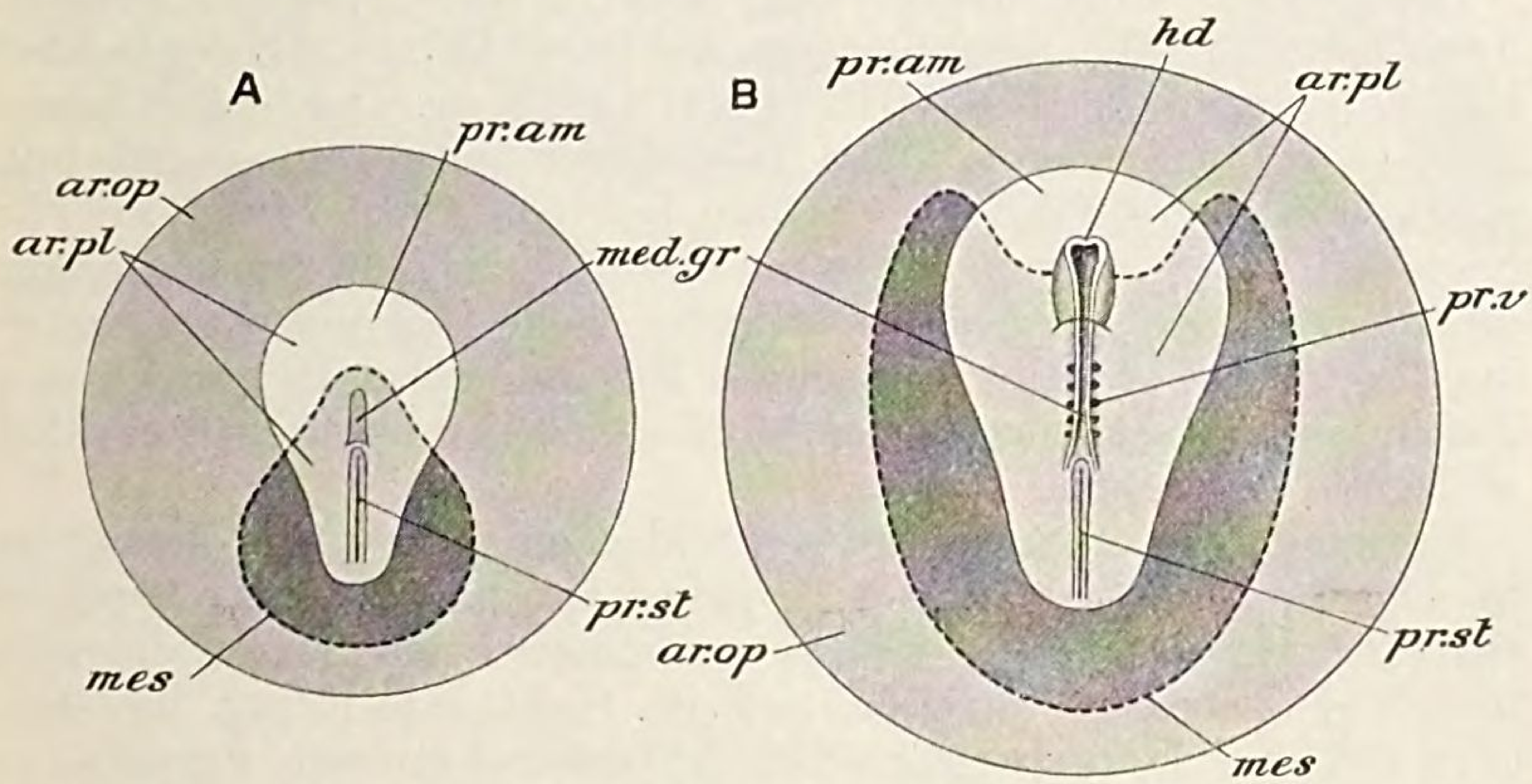


FIG. 1013.—**Gallus bankiva.** Two stages in the development of the blastoderm: diagrammatic. *ar. op.* area opaca; *ar. pl.* area pellucida; *hd.* head; *med. gr.* medullary groove; *mes.* mesoderm, indicated by dotted outline and deeper shade; *pr. am* pro-amnion; *pr. st.* primitive streak; *pr. v.* proto-vertebræ. (From Marshall's *Embryology*.)

area opaca (*ar. op.*), and is formed of a superficial layer of ectoderm having below it a somewhat irregular aggregation of lower-layer cells, which gradually become differentiated into mesoderm and endoderm.

At the posterior end of the blastoderm a delicate, longitudinal, grooved mark, the *primitive streak* (*pr. st.*) makes its appearance. Like the similarly named structure in the Frog, it represents the blastopore, but no invagination takes place beyond a solid ingrowth of ectoderm, and the enteric cavity is formed entirely by the folding in of the ventral walls of the embryo.

Immediately in front of the primitive streak the *medullary groove* (*med. gr.*) appears, and the *medullary folds* which bound it on the right and left diverge posteriorly, so as to embrace the anterior end of the primitive streak, in just the same way as they

embrace the blastopore in Amphioxus. Both primitive streak and medullary groove lie at right angles to the long axis of the egg, the broad end of the latter being to the embryo's right.

The blastoderm gradually extends peripherally, so as to cover the yolk, and thereby becomes divisible into an *embryonic portion*, from which the embryo is formed, and an *extra-embryonic portion* which invests the yolk-sac, and takes no direct share in the formation of the embryo. The extension of the ectoderm and endoderm takes place regularly and symmetrically, but the mesoderm, while extending equally in the lateral and posterior regions, grows forwards in the form of paired extensions, which afterwards unite, so that for a time there is an area of the blastoderm in front of the head of the embryo, formed of ectoderm and endoderm only, and called the *pro-amnion* (*pr. am.*).

At an early period the *vertebral plate* or dorsal portion of mesoderm bounding the medullary groove (p. 114) becomes segmented into protovertebræ (Figs. 1013, B, and 748, B, *pr. v.*); and the *lateral plate* or ventral portion of the same layer splits into somatic and splanchnic layers with the cœlome between (Fig. 748, B). The notochord (*nch.*) is developed in the middle line below the medullary groove: sometimes it arises directly from the endoderm, as in most of the lower forms, sometimes the mesoderm is formed as a continuous plate, the axial portion of which is subsequently divided off as the notochord.

Gradually the embryo becomes folded off from the yolk-sac, as in other large-yolked eggs, but, owing apparently to the confined space in which it is enclosed, it soon turns over, so as to lie with its left side against the yolk, and its right side facing the shell (Fig. 1015). The body (Fig. 1014, A) becomes strongly flexed so as to bring the head and tail into contact, and the head soon acquires a proportionally immense size, with very large projecting eyes. At first the head is quite like that of the lower vertebrate embryos, with protuberant brain-swellings (*f. br.*, *m. br.*, *h. br.*), large square mouth, ventrally placed nostrils connected by grooves with the mouth, and three or four pairs of gill-slits. As in Reptiles, there is never any trace of gills. In the Ostrich and Apteryx, as well as in some Carinatæ, an opercular fold grows backwards from the hyoid arch, and covers the second and third branchial clefts. Soon the margins of the mouth grow out into a beak (Fig. 1014, B), the clefts close, with the exception of the first, which becomes the tympano-eustachian passage, and the head becomes characteristically avian. The limbs are at first alike in form and size (A, *f. l.*, *h. l.*) and the hands and feet have the character of paws, the former with three, the latter with four digits, but gradually the second digit of the hand outgrows the first and third, producing the characteristic avian manus (B), while the metatarsal region elongates and gives rise to the equally characteristic foot. At the same time feather-

papillæ make their appearance, arranged in narrow and well-defined pterylæ.

At an early period capillaries appear in the extra-embryonic blastoderm between the opaque and pellucid areas, and give rise

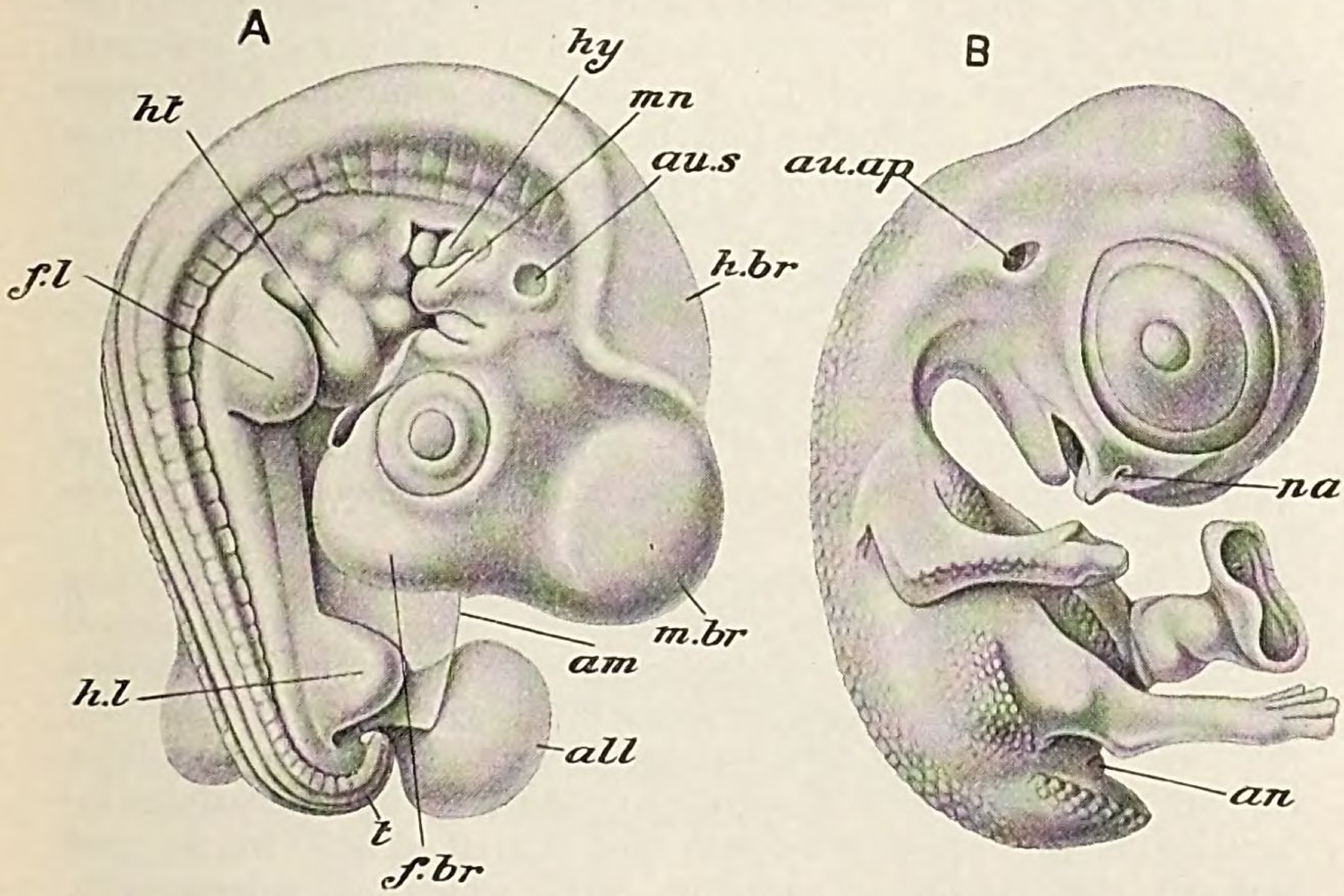


FIG. 1014.—**Gallus bankiva.** Two stages in the development of the embryo. *all.* allantois; *am.* cut edge of amnion; *an.* anus; *au. ap.* auditory aperture; *au. s.* auditory sac; *f. br.* fore-brain; *f. l.* fore-limb; *h. br.* hind-brain; *h. l.* hind-limb; *ht.* heart; *hy.* hyoid arch; *m. b.* mid-brain; *mn.* mandibular arch; *na.* nostril; *t.* tail. (After Duval.)

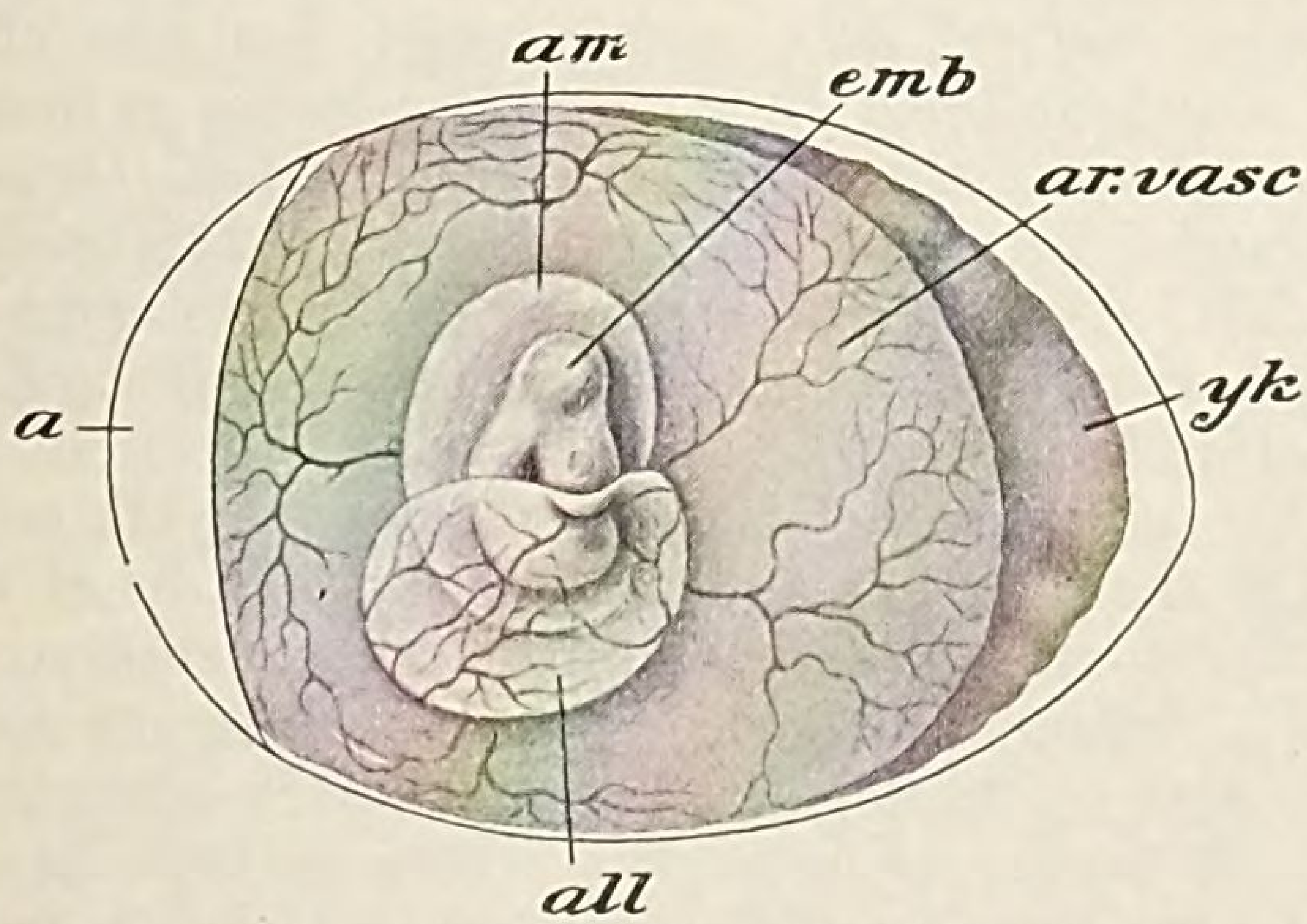


FIG. 1015.—**Gallus bankiva.** Egg with embryo and fœtal appendages. *a.* air-space; *all.* allantois; *am.* amnion; *ar. vasc.* area vasculosa; *emb.* embryo; *yk.* yolk-sac. (After Duval.)

to a well-defined *area vasculosa* (Fig. 1015, *ar. vasc.*): they are supplied by *vitelline arteries* from the dorsal aorta, and their blood is returned by *vitelline veins* which join the portal vein and take the

blood, through the liver, to the heart. The vascular area gradually extends until it covers the whole of the yolk-sac: its vessels take an important share in the absorption of the yolk by the embryo.

Before the embryo has begun to be folded off from the yolk the rudiment of one of the two characteristic *embryonic membranes*, the *amnion*, has appeared. A crescentic *amniotic fold* arises (Fig. 1016, A, *am. f.*), in front of the head-end of the embryo, from the region of the pro-amnion: it consists at first of ectoderm only, the mesoderm not having yet spread into the pro-amnion. The fold is soon continued backwards along the sides of the body (B) and round the tail (A), but in these regions (*am. f'.*) it consists from the first of ectoderm *plus* the somatic layer of mesoderm, *i.e.*, it is a fold of what may be called the extra-embryonic body-wall. The cavity is a prolongation of the space between the somatic and splanchnic layers of mesoderm, *i.e.*, is an extension of the extra-embryonic cœlome.

The entire amniotic fold gradually closes in above (C), forming a double-layered dome over the embryo. Its inner layer, formed of ectoderm internally and mesoderm externally, is the *amnion* (*am.*), the cavity of which becomes filled with a watery *amniotic fluid*, serving as a protective water-cushion to the enclosed embryo. Its outer layer, formed of ectoderm externally and mesoderm internally, is the *serous membrane* (*sr. m.*): it comes to lie just beneath the vitelline membrane, with which it subsequently fuses

The second of the embryonic membranes, the *allantois*, is developed as an outpushing of the ventral wall of the mesenteron at its posterior end (C, *all.*), and consists, therefore, of a layer of splanchnic mesoderm lined by endoderm. It has at first the form of a small ovoid sac having the precise anatomical relations of the urinary bladder of Amphibia (Fig. 1014, A, *all.*). It increases rapidly in size (Fig. 1015, *all.*), and makes its way, backwards and to the right, into the extra-embryonic cœlome, between the amnion and the serous membrane (Fig. 1016, C, D). Arteries pass to it from the dorsal aorta, and its veins, joining with those from the yolk sac, take the blood through the liver to the heart. Next, the distal end of the sac spreads itself out and extends all round the embryo and yolk-sac (D, *all'.*), fusing, as it does so, with the serous and vitelline membranes, and so coming to lie immediately beneath the shell-membrane. It finally encloses the whole embryo and yolk-sac, together with the remains of the albumen, which has, by this time, been largely absorbed. The allantois serves as the embryonic respiratory organ, gaseous exchange readily taking place through the porous shell; its cavity is an embryonic urinary bladder, excretory products being discharged into it from the kidneys.

At the end of incubation the embryo breaks the shell, usually by

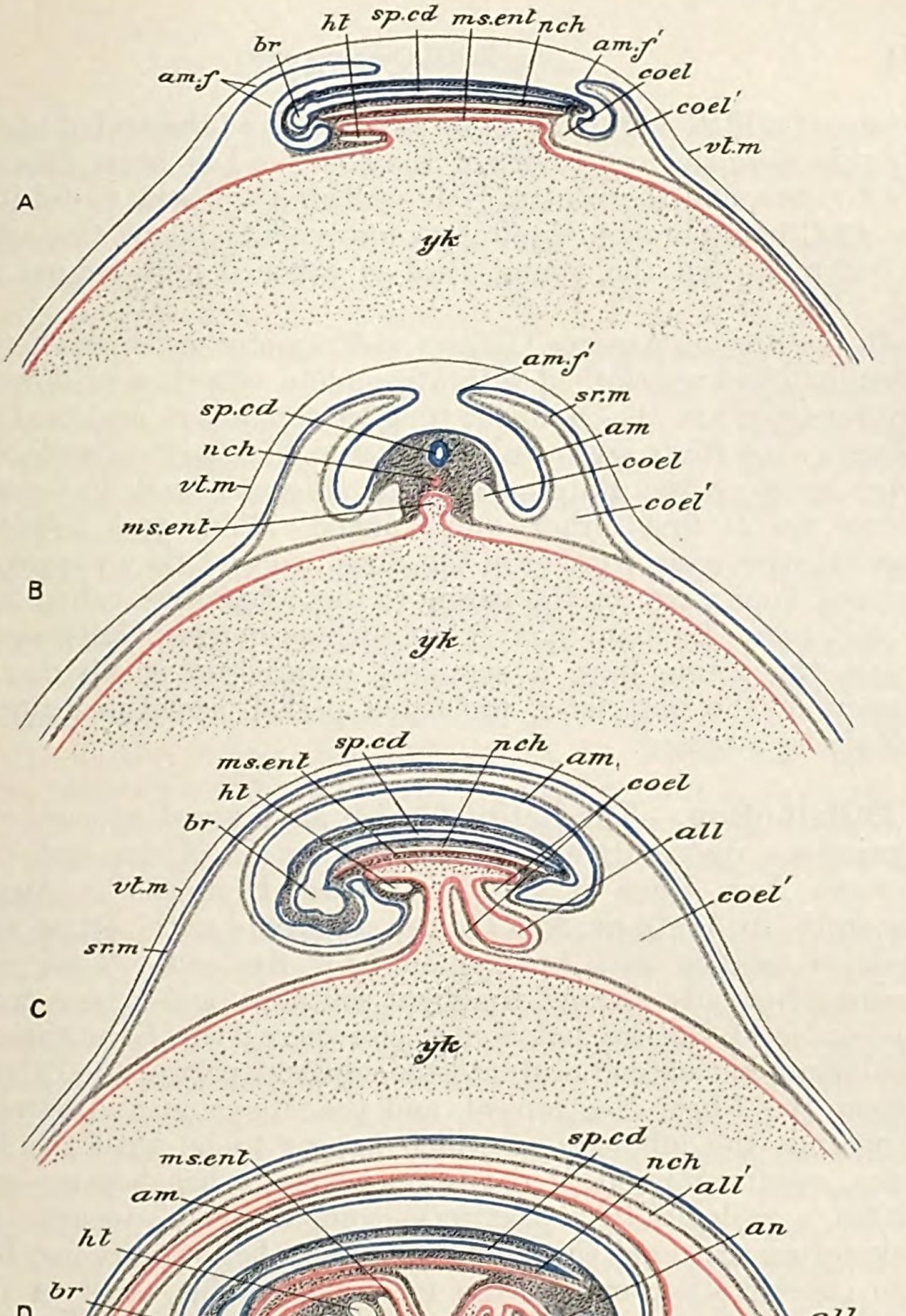


FIG. 1016.—Diagrams illustrating the development of the fœtal membranes of a **Bird.** A, early stage in the formation of the amnion, sagittal section; B, slightly later stage, transverse section; C, stage with completed amnion and commencing allantois; D, stage in which the allantois has begun to envelop the embryo and yolk-sac. The ectoderm is represented by a blue, the endoderm by a red line; the mesoderm is grey. *all.* allantois; *all'.* the same growing round the embryo and yolk-sac; *am.* amnion; *am.f.*, *am.f.'* amniotic fold; *an.* anus; *br.* brain; *cœl.* cœlome; *cœl'.* extra-embryonic cœlome; *ht.* heart; *ms.ent.* mesenteron; *mth.* mouth; *nch.* notochord; *sp.cd.* spinal cord; *sr.m.* serous membrane; *umb.d.* umbilical duct; *vt.m.* vitelline membrane; *yk.* yolk-sac.

means of a little horny elevation or *caruncle* at the end of the beak. By this time the remainder of the yolk-sac has been drawn into the cœlome, and the ventral body-walls have closed round it. On the shell being broken respiratory movements begin, the aperture is enlarged, and the young Bird is hatched and begins a free life.

In the Ratitæ, Anseres, Gallinæ, and some other Birds the young when hatched are clothed with a complete covering of down or of feathers, and are able from the first to run about and feed themselves; such Birds are called *Præcoces* or *Nidifugæ*. In the higher types, such as the Rapacious Birds, Pigeons, and Passeres, the young are at first either quite naked, blind, and helpless, or covered with mere patches of soft down, so that they require to be fed and kept warm by the parents; these forms are called *Altrices* or *Nidicolæ*. In many Sea Birds, such as Petrels, Gulls, and Penguins, the young have a complete covering of woolly down, but remain in the nest for a prolonged period, sometimes until the full size is attained.

Distribution.—The Ratitæ furnish an interesting case of discontinuous distribution. Struthio occurs in Africa and South-western Asia, Rhea in South America, Dromæus in Australia, Casuarius in Australia, New Guinea, and some of the other Austro-Malayan islands, and Apteryx in New Zealand. Thus taking recent forms only, each of the great southern land-masses contains one order of Ratitæ not found elsewhere; the Struthiones are Ethiopian, but extend also into the adjacent part of the Palæarctic region, the Rheæ Neotropical, and the Megistanes Australasian. Æpyornis, the affinities of which appear to be with the Megistanes, occurs only in Madagascar, where it has become extinct within — geologically speaking — comparatively recent times. Taking the scattered distribution of the above-mentioned Ratitæ into consideration, one of the most remarkable facts in distribution is the occurrence, in the limited area of New Zealand, of no fewer than six genera and between twenty and thirty species of Dinornithidæ or Moas, some of which became extinct so short a time ago that their skin, flesh, feathers, dung, and egg-shells are preserved.

Among the Carinatæ the Penguins are exclusively southern, occurring only in the South Temperate and Arctic Oceans. They may be said to be represented in the Northern Hemisphere by the Puffins and Auks, one of which, the Great Auk or Gare-fowl (*Alca impennis*) was actually impennate, its wings being converted, as in the Penguins, into paddles. The Crypturi (Tinamous) are exclusively Neo-tropical, the Humming-birds American, the Birds of Paradise and Bower-birds Australian and Austro-Malayan. Amongst negative facts, the Psittaci or Parrots are characteristically absent

in the Palæarctic and most of the Neartic region, the Finches in the Australasian region, as well as in New Zealand and Polynesia, and the Starlings in both regions of the New World.

Birds are comparatively rare in the fossil state: their powers of flight render them less liable to be swept away and drowned by floods and so imbedded in deposits at the mouths of rivers or in lakes. Up to the cretaceous period, Archæopteryx, from the Lower Jurassic, is the only Bird known. In the Cretaceous of North America toothed Birds of the orders Odontolcæ and Ichthyornithes make their appearance, while in the Eocene numerous interesting forms occur, including the Gastornithes and the Stereornithes.

Ethology.—It is impossible here to do more than allude, in the briefest way, to the immense and fascinating group of facts relating to the instincts, habits, and adaptations found in the present class. Their social instincts, their song, their courtship customs, the wonderful advance in the parental instinct, leading to diminished mortality in the young, are all subjects for which the reader must be referred to the works on general Natural History mentioned in the Appendix. The same applies to the puzzling subject of migration, which will be referred to in the Section on Distribution.

Phylogeny.—That Birds are descended from Reptilian ancestors, that they are, as it has been said, "glorified Reptiles," seems as certain as anything of the kind can well be. Apart from the direct evidence afforded by Archæopteryx and by the numerous avian characteristics of Dinosauria and Ornithosauria, the indirect evidence of anatomy and embryology is very strong. The single occipital condyle, the six bones to each mandibular ramus, the ankle-joint between the proximal and distal tarsals, the number of phalanges in the digits of the foot, the epidermal exoskeleton, partly taking the form of scales, the meroblastic egg with large food yolk, the amnion, and the respiratory allantois, are all characters common to Birds and Reptiles and not found together, indeed for the most part not found at all, in any other class. For this reason Reptiles and Birds are often conveniently grouped together, as already stated (p. 291), as *Sauropsida*.

It seems probable that the earliest Birds could fly, and that their evolution from Reptilian ancestors was directly connected with the assumption of aërial habits. It is not unlikely that these ancestors possessed a patagium, like that of Ornithosauria, and that, as the scales of the fore-limb developed into feathers, this organ was gradually reduced to the small pre- and post-patagia of the existing Bird's wing. What was the nature of the Reptilian ancestor is a question as yet quite unsolved. It can hardly have been a Pterodactyle, since in that order the modification of the fore-limb has proceeded on entirely different lines from those which charac-

terise Birds; it cannot well have been a Dinosaur, since we have no evidence that any member of that order was arboreal, or showed the least tendency on the part of the fore-limb to assume the wing-form. Nevertheless the skull and brain of Ornithosauria and the pelvis and hind-limb of many Dinosauria show such approximation to avian characters as can hardly be without significance.

Probably the earliest Birds were all, in the etymological sense, Carinatæ, *i.e.*, had the sternum provided with a keel for the attachment of the pectoral muscles. Probably, also, they all possessed teeth, and had diverged into well-marked orders before those organs were lost. The Odontolcæ, for instance, have their nearest allies in the Divers (Pygopodes), while the Ichthyornithes resemble the Terns, members of the widely separated order Gaviæ.

In several existing types of Carinatæ the power of flight is wanting, and in all such cases it is practically certain that flightlessness is due to the degeneration of the wings; in other words, that the ancestors of the Penguins, Great Auk, Dodo, Weka (Ocydromus), Kakapo (Stringops), &c., were ordinary flying Birds. In the Penguins and the Great Auk the wings have simply undergone a change of function, being converted into paddles, and consequently the only parts of them which have degenerated are the feathers; but in the other forms referred to the wing has become more or less functionless, and hence has diminished in size, while the partial atrophy of the muscles has resulted in a more or less complete reduction of the carina sterni and furcula and an increase of the coraco-scapular angle. Now it is by an exaggeration of these peculiarities that the Ratitæ are distinguished from the Carinatæ, and there is every reason for thinking that they also are the descendants of flying Birds, and that their distinctive characters—absence of locking apparatus in the feathers, flat sternum, wide coraco-scapular angle, &c.—are all due to degeneration correlated with disuse of the wings. From the fact that the dromæognathous skull is more reptilian than any other type, it would seem that the Ratitæ diverged early from the carinate stock. From the fact that, in the structure of the skull and pelvis, the Ostrich and Rhea are widely separated both from one another and from the Australasian Ratitæ, it seems probable that the three orders of Ratitæ arose independently from primitive Carinatæ, and that the entire division is to be looked upon as a *convergent* or *polyphyletic* group, owing its distinctive characters, not to descent from a common ancestor, but to the independent acquisition of similar characters under the influence of like surroundings.

The question of the phylogeny of the orders of Carinatæ is far too complex to be discussed here. Suffice it to say that the Ichthyornithes, Odontolcæ, Impennes, Pygopodes, and Crypturi are to be looked upon as the lowest or most generalised orders, while the highest or most specialised are the Psittaci, the Accipitres, the

Striges, the Picariæ, and especially the Passeres. Among the latter the Corvidæ (Crows) are probably to be looked upon as the most exalted members of the class (Fig. 1016 *bis*).

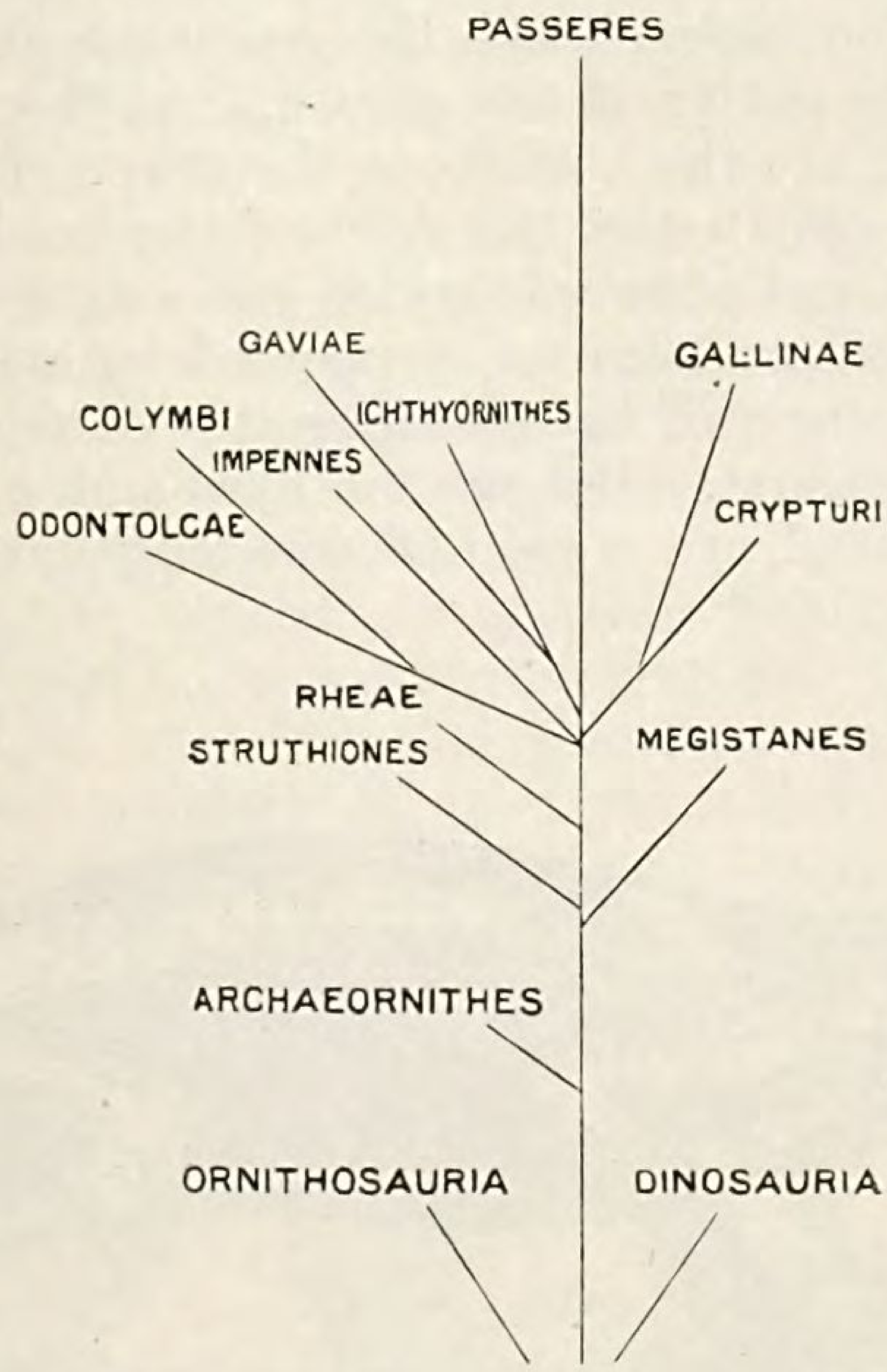


FIG. 1016 *bis*.—Diagram illustrating the Relationships of the chief groups of Birds.

CLASS VI.—MAMMALIA.

The class Mammalia, the highest of the Vertebrata, comprises the Monotremes and Marsupials, the Hoofed and Clawed Quadrupeds, the Whales and Porpoises and Sea-Cows, the Rodents, Bats and Insectivores, the Lemurs and Apes, and the Human Species. All Mammals, though many are aquatic, are air-breathers throughout life, lungs being, as in Reptiles and Birds, the sole organs of respiration. The blood of Mammals has a high temperature, resembling in that respect the blood of Birds, and differing from that of Reptiles and Amphibia. The scales of Reptiles and the feathers of Birds are replaced in Mammals by peculiar epidermal structures, the hairs, usually developed in such quantities as to form a thick soft covering or fur. The young are nourished after birth by the secretion of mammary or milk glands.

1. Example of the Class—The Rabbit (*Lepus cuniculus*).

External Characters.—The Rabbit (Fig. 1017) is a four-footed or quadrupedal animal, having the whole surface of its

body covered with soft fur. The head bears below its anterior extremity the mouth, in the form of a transverse slit bounded by soft lips. The upper lip is divided by a longitudinal cleft, running backwards to the nostrils, and exposing the chisel-shaped *incisor teeth.* Behind the incisor teeth the hairy integument projects on each side into the cavity of the mouth. At the end of the snout, above the mouth, are the nostrils, in the shape of two oblique slits. The large eyes, situated at the sides of the head, have each three eyelids, an upper and a lower hairy lid, and an anterior hairless third eyelid or *nictitating membrane,* supported by a plate of cartilage. *Vibrissæ*—very long stiff hairs—are scattered above and below the eyes and on the snout. Behind the eyes and a little nearer the summit of the head, are a pair of very long flexible and movable

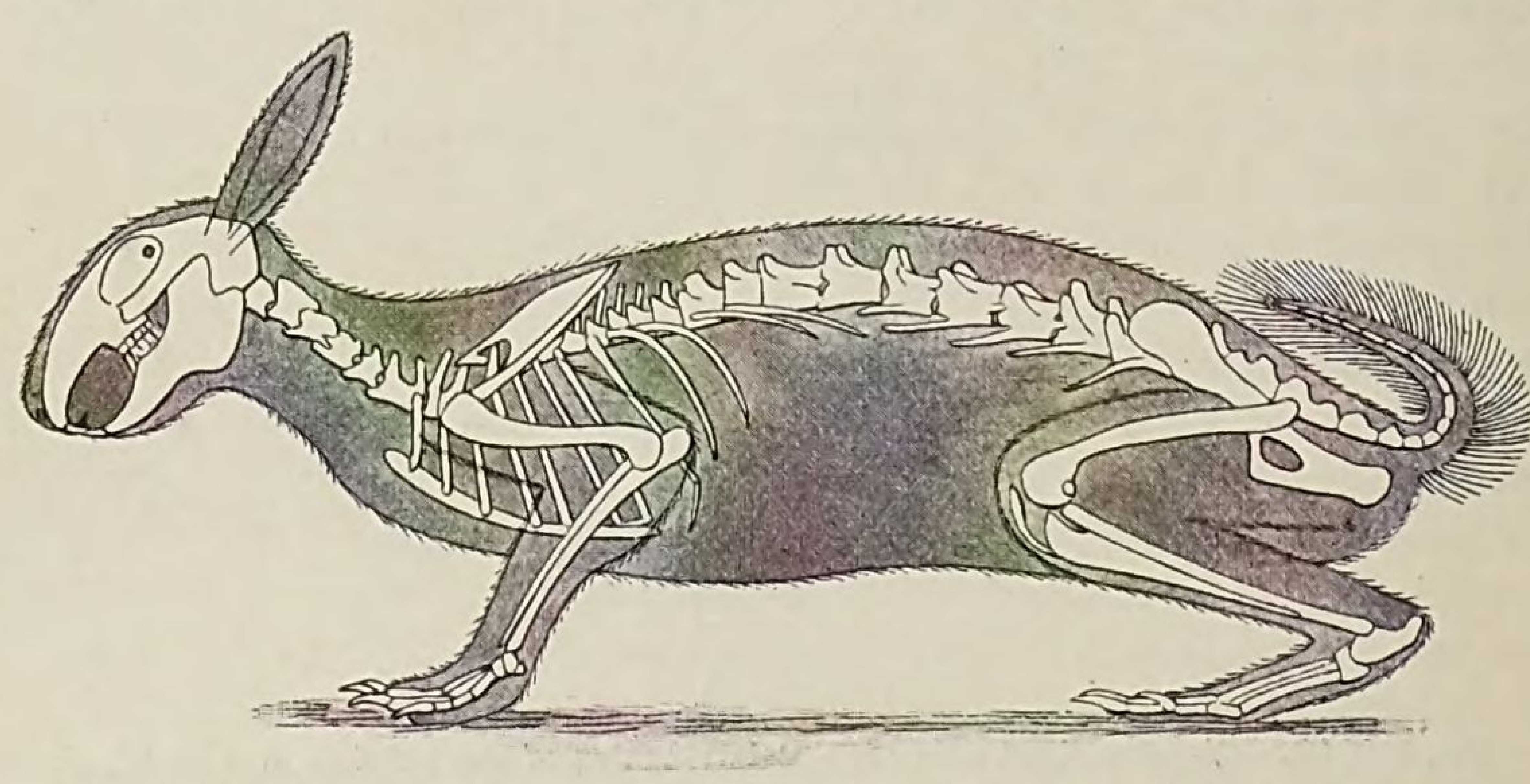


FIG. 1017.—**Lepus cuniculus.** Lateral view of skeleton with outline of body.

external ears or *pinnæ.* These are somewhat spout-shaped, expanding distally, and are usually placed vertically with the concavity, directed laterally and somewhat forwards, leading to the external auditory opening. The *neck* is a distinct constriction, but relatively short as compared with the neck of the Pigeon. The *trunk* is distinguishable into *thorax* in front and *abdomen* behind. On the ventral surface of the abdomen in the female are four or five pairs of little papillæ—the *teats.* At its posterior end, below the root of the tail, is the *anal opening.* and in front of this in the male is the *penis,* with a small terminal *urinogenital aperture,* and with the *testes,* each in a prominent *scrotal sac,* at the sides : and in the female the opening of the *vulva.* In the space (*perinæum*) between anus and penis or vulva are two bare, depressed areas of skin into which open the ducts of certain glands—the *perinæal glands*—with a secretion having a strong and characteristic odour. The *tail* is very short and covered with a tuft of fluffy fur.

The *fore* and *hind limbs,* both of which take part in locomotion and in supporting the weight of the animal, differ considerably in

size—the fore limbs being much shorter than the hind limbs. Both have the same general divisions as in the Lizard. The upper arm is almost completely hidden by the skin, being applied closely against the side of the body. The *manus* is provided with five digits, each terminating in a horny claw. The thigh is also almost hidden by the skin; the *pes* has four digits only, all provided with claws.

Skeleton.—The *spinal column* of the Rabbit is divisible, like that of the Pigeon and the Lizard, into five regions—the cervical, the thoracic, the lumbar, the sacral, and the caudal. In the *cervical* region there are seven vertebræ; in the *thoracic* twelve or sometimes thirteen, in the *lumbar* seven, or sometimes six, in the *sacral* four, and in the *caudal* about fifteen.

The centra of the vertebræ in a young Rabbit consist of three parts—a middle part which is the thickest, and two thin disks of bone—the *epiphyses*—anterior and posterior, applied respectively to the anterior and posterior faces of the middle part or centrum proper. Between successive centra in an unmacerated skeleton are thin disc-like plates of fibro-cartilage—the *inter-vertebral discs.*

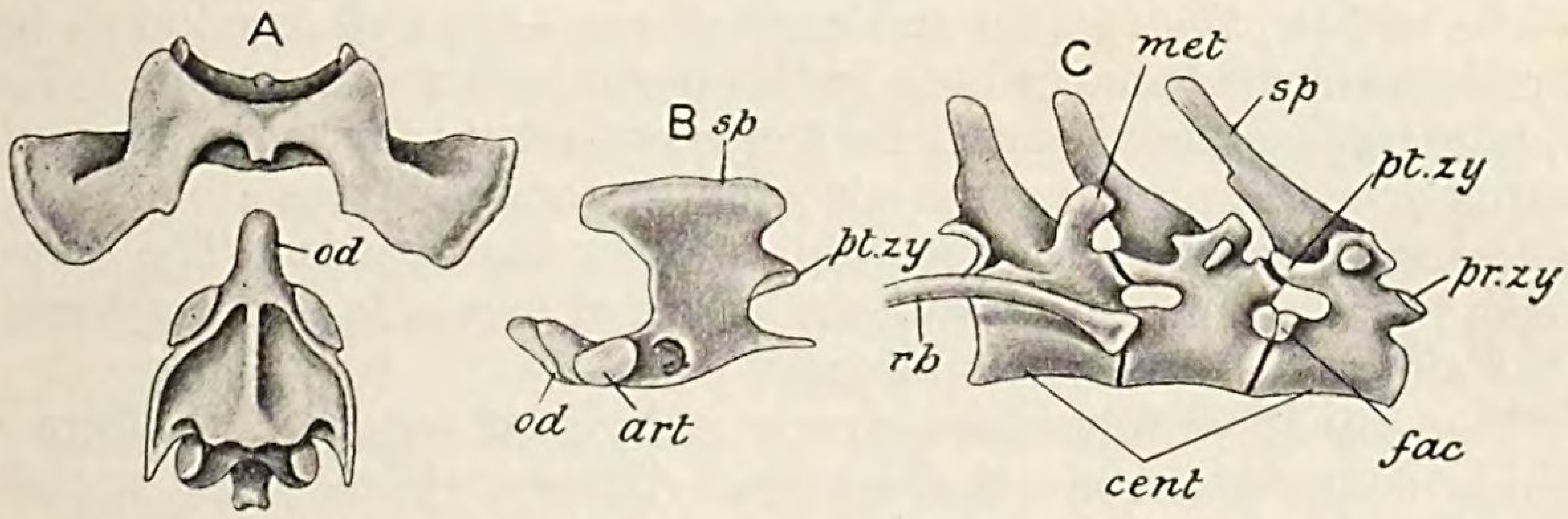


FIG. 1018.—**Lepus cuniculus.** *A*, atlas and axis, ventral aspect *od.* odontoid process of axis. *B*, lateral view of axis; *art.* articular facet for occipital condyle; *od.* odontoid process; *pt.zy.* post-zygapophysis; *sp.* neural spine. *C*, thoracic vertebræ, lateral view. *cent.* centrum; *fac.* facet for rib; *met.* metapophysis; *pr.zy.* prezygapophysis; *pt.zy.* post-zygapophysis; *rb.* rib; *sp.* spinous process.

The first vertebra or *atlas* (Fig. 1018, *A*) resembles the corresponding vertebra of the Pigeon in being of the shape of a ring without any solid centrum like that of the rest. On the anterior face of its lateral portions are two concave articular surfaces for the two condyles of the skull. The second vertebra or *axis* (*A* and *B*) bears on the anterior face of its centrum a peg-like process—the *odontoid process* (*od.*)—which fits into the ventral part of the ring of the atlas: it has a compressed spine (*sp.*), produced in the antero-posterior direction; its transverse processes are short and perforated by a canal for the vertebral artery. All the rest of the cervical vertebræ have their transverse processes bifurcated and perforated at their bases by the canal—*vertebrarterial canal*—for the vertebral artery. The seventh cervical differs from these

in having a more elongated neural spine, in having its transverse processes simple and without perforation for the vertebral artery, and in the presence on the posterior edge of the centrum of a little concave semi-lunar facet.

The thoracic vertebræ (*C*) have elongated spines which are mostly directed backwards as well as upwards. The transverse processes are short and stout; each bears near its extremity a small smooth articular surface or *tubercular facet* for the tubercle of a rib. On the anterior and posterior borders of each vertebra is a little semi-lunar facet, the *capitular facet* (*fac.*), situated at the junction of the centrum and the neural arch. The two contiguous semi-lunar facets of successive vertebræ form between them a little cup-like concavity into which the head or *capitulum* of a rib is received. The semi-lunar facet on the last cervical vertebra forms with that on the anterior border of the first thoracic the concavity for the head of the first rib.

In the lumbar region the spines are comparatively short, and both transverse processes and bodies are devoid of facets. From the centrum of each of the first two projects downwards a short flattened process—the *hypapophysis*. Certain accessory processes —the *metapophyses* (*met.*) and *anapophyses*—are well developed, the former being extremely long in the posterior lumbar region. The metapophyses are situated in front, projecting forwards and outwards over the prezygapophysis; and the anapophyses are situated below the post-zygapophyses and project backwards. The transverse processes are long, and are directed forwards and outwards; that of the last lumbar is bifurcate.

The sacral vertebræ are firmly ankylosed together to form a single composite bone, the *sacrum*. The vertebræ bear a close resemblance to those of the lumbar region, but the hypapophyses and anapophyses are wanting, and the metapophyses are comparatively small. The first and second bear great expanded lateral plates—sacral ribs—with roughened external surfaces for articulation with the ilia.

Of the caudal vertebræ the more anterior resemble those of the sacral region, and have similar processes; but as we pass backwards in the caudal region all the processes gradually diminish in size, the most posterior vertebra being represented merely by nearly cylindrical centra.

There are twelve pairs of *ribs*, of which the first seven are known as true ribs, *i.e.* are connected by their cartilaginous sternal ribs with the sternum; while the remaining five, the so-called false or floating ribs, are not directly connected with the sternum. All, except the last four, bear two articular facets, one on the vertebral extremity or *capitulum*, and the other on a little elevation or *tubercle* situated at a little distance from this, the former for the bodies, the latter for the transverse processes of the vertebræ.

The sternum (Fig. 1020) consists of six segments or *sternebræ*, the first, the *manubrium sterni* or *presternum*, is larger than the rest, and has a ventral keel. With the last is connected a rounded cartilaginous plate, the *xiphisternum*.

The *skull* (Fig. 1019), if we leave the jaws out of account, is not at all unlike that of the Pigeon in general shape. The length is great as compared with either the breadth or the depth; the maxillary region, or region of the snout (corresponding to the beak of the Pigeon), is long in proportion to the rest, the orbits closely approximated, being separated only by a thin inter-orbital partition, and the optic foramina united into one. But certain important differences are to be recognised at once. One of these is in the mode of union of the constituent bones. In the Pigeon, as we have seen, long before maturity is attained, the bony elements of the skull, originally distinct, become completely fused together so that their limits are no longer distinguishable. In the Rabbit, on the other hand, such fusion between elements only takes place in one or two instances, the great majority of the bones remaining distinct throughout life. The lines along which the edges of contiguous bones are united—the *sutures* as they are termed—are sometimes straight, sometimes wavy, sometimes zig-zagged, serrations of the edges of the two bones interlocking; in some cases the edges of the bones are bevelled off and the bevelled edges overlap, forming what is termed a *squamous* suture.

Another conspicuous difference between the skull of the Rabbit and that of the Pigeon is in the mode of connection of the lower jaw, which in the former articulates directly with the skull, the quadrate, through which the union is effected in the Pigeon, being apparently absent. Certain large apertures which are distinguishable are readily identified with the large openings in the skull of the Pigeon. In the posterior wall of the skull is a large rounded opening, the *foramen magnum*, flanked with a pair of smooth rounded elevations or *condyles* for articulation with the first vertebra, these obviously corresponding to the single condyle situated in the middle below the foramen in the Pigeon. A large opening, situated at the end of the snout and looking forwards, obviously takes the place of the *external nares* of the Pigeon; and a large opening in the roof of the mouth leading forward to the external nasal opening, plainly represents, though much wider and situated further back, the *internal* or *posterior nares* of the Pigeon; while the rounded tubular opening (*aud. me.*) situated at the side of the posterior part of the skull, some distance behind the orbit, is evidently the same as the *auditory aperture* of the Pigeon.

Surrounding the large opening of the foramen magnum are the bones of the *occipital* region of the skull, the *supra-*, *ex-* and *basi-occipitals*. The first of these (*s. oc.*) is a large plate of bone whose external surface is directed backwards and upwards, and elevated in the middle into a shield-shaped prominence. The *ex-occipitals*

lie at the sides of the opening, and each bears the greater part of the somewhat oval prominence or *condyle* with which the corresponding surface of the atlas or first vertebra articulates. Each is produced below into a process called the *par-occipital* (*par. oc.*), closely applied to the tympanic bulla. At the end of this, imbedded in the tendon of a muscle, the *stylo-glossus*, is a small bony rod, the *stylo-hyal*. A small aperture, the *condylar foramen*, situated below the condyle, is for the passage of one of the cranial nerves, the *hypo-glossal*. The *basi-occipital* is a median plate of bone, almost horizontal in position, which forms the floor of the most posterior part of the cranial cavity; it bears the lower third of the occipital condyles. All these four bones of the occipital region are in the adult Rabbit united together to form the single *occipital bone*. Articulating in front with the basi-occipital is a plate of bone, also horizontal in position, which forms the middle part of the floor of the cranial cavity. This is the *basi-sphenoid*; it is perforated at about its middle by an oval foramen, and on its upper surface is a depression, the *sella turcica*, or *pituitary fossa*, in which the pituitary body rests. In front of it is another median bone of laterally compressed form, the *presphenoid*, with which it is connected by cartilage, the removal of which leaves a gap in the dried skull; the presphenoid forms the lower boundary of the single large *optic foramen* (*opt. fo.*). Connected laterally with the basi-sphenoid and pre-sphenoid are two pairs of thin irregular plates, the *ali-sphenoid* (*as.*) behind and the *orbito-sphenoid* (*o. sph.*) in front. The ali-sphenoids are broad wing-like bones, each produced below into a bilaminate process, the *pterygoid* process. A large foramen, the *sphenoidal fissure*, situated between the basi-sphenoid and the alisphenoid of each side, transmits from the interior of the skull the third and fourth cranial nerves, the first and second divisions of the fifth, and the sixth nerves.

The boundary of the anterior part of the brain case is completed by a narrow plate of bone, the *cribriform plate* of the *ethmoid*, perforated by numerous small foramina for the passage of the olfactory nerves. This cribriform plate forms a part of a median vertical bone, the *mesethmoid*, the remainder of which, or *lamina perpendicularis*, forms the bony part of the partition (completed by cartilage in the unmacerated skull) between the nasal cavities. Fused with the mesethmoid are two lateral, thin, twisted bones, the *ethmo-turbinals*, and with its inferior edge articulates a long median bone with a pair of delicate lateral wings, the *vomer*. None of these, with the exception of the cribriform plate, take any share in the bounding of the cavity of the cranium. Roofing over the part of the cranial cavity, the walls and floors of which are formed by the sphenoid elements, is a pair of membrane bones, the *parietals* (*pa.*), and further forward another pair, the *frontals* (*fr.*). The parietals are plate-like bones, convex externally, concave internally, which articulate with the supra-occipital behind by a

transverse serrated suture, the *lambdoidal* suture. The right and left parietals articulate together by means of a somewhat wavy

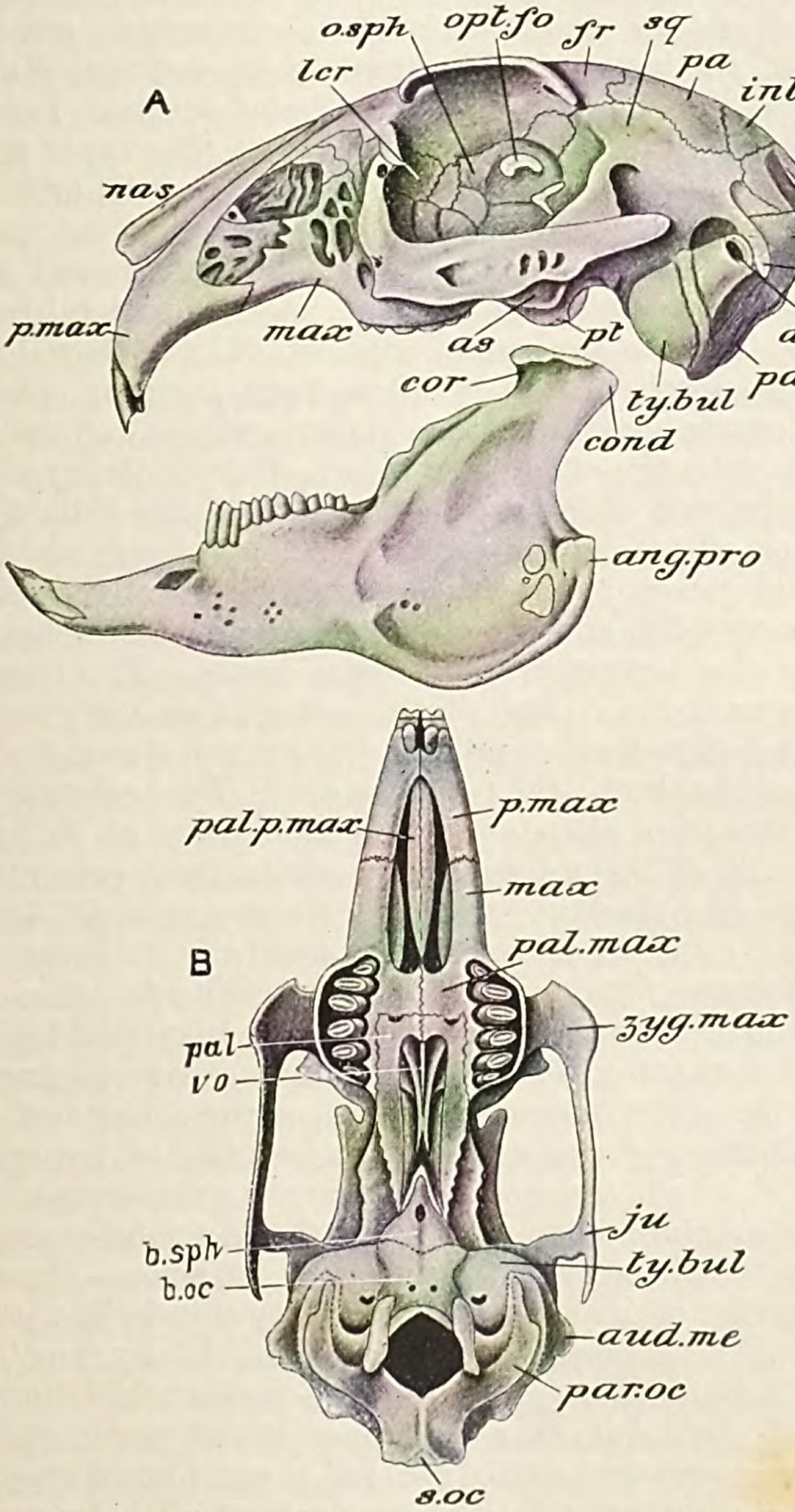


Fig. 1019.—**Lepus cuniculus.** Skull. *A*, lateral view; *B*, ventral view. *ang. proc.* angular process of mandible; *as.* alisphenoid (external pterygoid process); *b. oc.* basi-occipital; *b. sph.* basisphenoid; *cond.* condyle; *fr.* frontal; *int.pa.* inter-parietal; *ju.* jugal; *lcr.* lacrymal; *max.* maxilla; *nas.* nasal; *opt. fo.* optic foramen; *o.sph.* orbito-sphenoid; *pa.* parietal; *pal.* palatine; *pal. max.* palatine plate of maxilla; *par.oc.* paroccipital process; *pal. p. max.* palatine process of pre-maxilla; *p. max.* pre-maxilla; *peri.* periotic; *pt.* pterygoid; *p. t. sq.* post-tympanic process of squamosal; *s.oc.* supra-occipital; *sq.* squamosal; *ty. bul.* tympanic bulla; *vo.* vomer; *zyg. max.* zygomatic process of maxilla.

suture, the *sagittal;* in front a transverse serrated suture, the *coronal*, connects them with the frontals. Between the supra

occipital and the parietals is a median ossification, the *inter-parietal* (*int. pa.*), which is not one of the essential elements of the vertebrate skull, but a representative of a class of bones—the so-called *Wormian bones*—intercalated in certain situations in the course of the sutures. The frontals are intimately united along the middle line by means of the *frontal* suture. Laterally their orbital plates form an important part of the upper portion of the inner wall of the orbit; above this, over each orbit, is a curved, somewhat crescentic process, the *supra-orbital process.* Between the ali-sphenoid below, the parietal and frontal above, the frontal and orbito-sphenoid in front, and the parietal behind, is a broad bone (*sq.*), the superior margin of which is bevelled off. This is the *squamosal.* It gives off in front a strong *zygomatic process,* which curves outwards, then downwards, and finally forwards, to unite with the jugal in the formation of the zygomatic arch. Below the root of the process is a hollow, the *glenoid fossa.* Behind it gives off a slender process, the *post-tympanic process* (*p. t. sq.*), which becomes applied to the outer surface of the periotic.

Between the occipital and parietal bones, below and behind the squamosal, are the *tympanic* and *periotic* bones. The tympanic forms the bony part of the wall of the external auditory meatus; below it is dilated to form a process (*ty. bul.*) projecting on the under surface of the skull—the *bulla tympani.* The periotic (*p. ot.*) is a bone of irregular shape enclosing the parts of the membranous labyrinth of the internal ear; externally it presents two small openings—the *fenestra ovalis* and *fenestra rotunda,*—visible only when the tympanic is removed; internally it bears a depression, the *floccular fossa,* for the lodgment of the flocculus of the cerebellum. The periotic and tympanic are not ankylosed together, and are loosely connected with the surrounding bones, being held in position by the post-tympanic processes of the squamosal. Between the tympanic and periotic are two foramina of importance, the *stylomastoid,* which transmits the seventh cranial nerve, and the *Eustachian aperture,* at which the Eustachian tube opens.

Roofing over the olfactory cavities are two flat bones—the *nasals* (*nas.*)—each having on its inner surface a very thin hollow process, the *naso-turbinal,* a detached part of the ethmoid. In front of the nasals are the pre-maxillæ (*p. max*)—large bones which form the anterior part of the snout, bear the upper incisor teeth, and give off three processes—a nasal, a palatine (*pal. p. max*), and a maxillary. The *maxillæ* (*max.*), which form the greater part of the upper jaw, and bear the pre-molar and molar teeth, are large, irregularly-shaped bones, the outer surfaces of which are spongy. They give off internally horizontal processes—the palatine processes (*pal. max*)—which unite to form the anterior part of the bony palate. Between the pre-maxillæ and maxillæ and the palatines on the lower surface of the skull is a large triangular opening divided into two—the *anterior palatine foramina*—by the palatine processes of the pre-

maxillæ. On the outer surface of each maxillæ, above the first pre-molar tooth, is a foramen—the *infra-orbital*—through which the second division of the fifth nerve passes. A strong process which is given off from the outer face of each maxilla and turns outwards and then backwards to unite with the zygomatic process of the squamosal and thus complete the zygomatic arch, is a separate bone in the young, the *malar* or *jugal* (*ju.*).

The maxillæ help to bound the nasal cavities externally, and each gives off on its inner aspect a pair of thin scroll-like bones—the *maxillo-turbinals*, which, like the naso-turbinals, are separated portions of the ethmoid. The rest of the narrow bony palate, forming the roof of the mouth and the floor of the nasal cavities, is formed by the *palatine plates* of the *palatine bones* (*pal.*). The *pterygoids* (*p.*) are small irregular bones, each of which articulates with the palatine in front and with the pterygoid process of the alisphenoid behind. The *lacrymals* (*lcr.*) are small bones, one situated in the anterior wall of each orbit, perforated by a small aperture—the *lacrymal foramen.*

In the interior of the skull are three cavities, the two olfactory or nasal cavities, right and left, in front, and the cranial cavity behind. The former are separated from one another by a median partition or septum, partly bony, partly cartilaginous, formed, as above described, by the *mesethmoid.* Each contains the turbinals or turbinated bones of its side; it opens on the exterior by the large external nasal aperture, and behind it communicates with the cavity of the mouth by the posterior nasal aperture.

The cranial cavity has its walls moulded to a considerable extent on the surface of the contained brain, and, in consequence, there are to be recognised concavities in the former corresponding with the prominent portions of the latter. These concavities are termed the *fossæ*, and they consist of the *cerebellar fossa* behind and the *cerebral fossa* in front, with the inconspicuous *olfactory fossa* in the frontal region.

The *mandible*, or lower jaw, consists of two lateral halves or rami, which articulate with one another in front by a rough articular surface or *symphysis*, while behind they diverge like the limbs of a letter V. In each ramus is a horizontal portion (anterior) which bears the teeth, and a vertical or ascending portion, which bears the articular surface or *condyle* (*cond.*) for articulation with the glenoid cavity of the squamosal; in front of the condyle is the compressed *coronoid process.* The angle where the horizontal and ascending processes meet gives off an inward projection or *angular process* (*ang. pro.*).

The *hyoid* consists, in addition to the separate vestigial stylo-hyals already mentioned (p. 422), of a stout thick body or *basi-hyal*, a pair of small anterior cornua or *cerato-hyals*, and a pair of long backwardly directed cornua or *thyro-hyals.*

The *auditory ossicles*, contained in the cavity of the middle ear,

and cut off from the exterior, in the unmacerated skull, by the tympanic membrane, are extremely small bones, which form a chain extending, like the columella auris of the Pigeon, from the tympanic membrane externally to the fenestra ovalis internally. There are three of these auditory ossicles—the *stapes*, which corresponds to the columella of the Pigeon; the *incus*, and the *malleus*, with a slender process—the *processus gracilis*. In addition there is a small disk-like bone, the *orbicular*, which is attached to the incus.

The elements of the *pectoral arch* (Fig. 1020) are fewer than in the Lizard. There is a broad thin triangular scapula, the base or vertebral edge of which has a thin strip of cartilage (the *supra-scapular* cartilage) continuous with it. Along the outer surface runs a ridge—the *spine*; the spine ends below in a long process—the *acromion process* (*a.*)—from which a branch process or *metacromion* (*ma.*) is given off behind. The part of the outer surface of the scapula in front of the spine is the *pre-spinous* or *pre-scapular fossa* (*af.*), the part behind the *post-spinous* or *post-scapular fossa* (*pf.*). At the narrow lower end of the scapula is a concave surface—the glenoid cavity—into which the head of the humerus fits, and immediately in front of this is a small inwardly curved process—the *coracoid process* (*c.*)—which is represented by two separate ossifications in the young Rabbit. A slender rod—the *clavicle* (*cl.*)—is connected with the acromion process externally and with the sternum internally by means of fibrous tissue. Attached to the outer end of the clavicle is a small cartilage, the *meso-scapula* (*mss.*), and connected with its inner extremity are two similar cartilages, which are supposed to represent the ventral portion of the *procoracoid* (*pc.*) and the *episternum* of the Sauropsida.

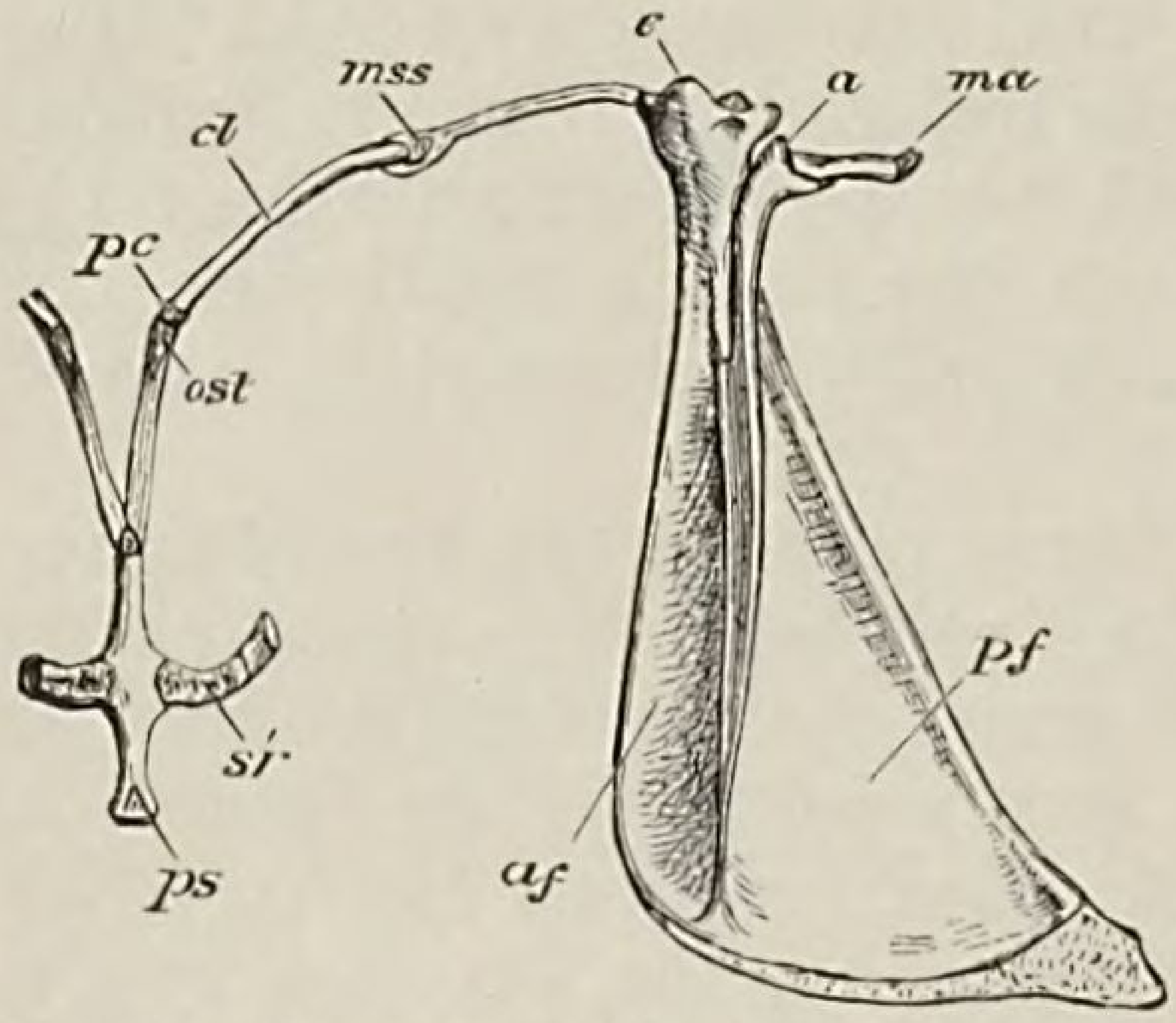


FIG. 1020.—**Lepus cuniculus.** Shoulder-girdle with anterior end of sternum of young specimen. *a.* acromion; *af.* pre-scapular fossa; *c.* coracoid; *cl.* ossified clavicle; *ma.* metacromion; *mss.* meso-scapular segment; *ost.* pro-sternum; *pc.* pre-coracoid; *pf.* post-scapular fossa; *sr.* sternal ribs. (After Flower.)

The skeleton of the fore-limb is more readily comparable with that of the Lizard than with that of the Bird; but there is a difference in the position of the parts owing to the rotation backwards of the distal end of the humerus, all the segments being thus brought into a plane nearly parallel with the median vertical plane of the body, with the pre-axial border directed outwards, and the original dorsal surface backwards. The radius and ulna are

fixed in the position of *pronation, i.e.*, the distal end of the radius is rotated inwards, so that, while the proximal end is external to the ulna, the distal end becomes internal, and the digits of the manus become directed forwards.

At the proximal end of the humerus are to be recognised: (1) A rounded *head* for articulation with the glenoid cavity of the scapula; (2) externally a *greater* and (3) internally a *lesser tuberosity* for the insertion of muscles; (4) a groove, the *bicipital groove*, between the two tuberosities. On the anterior surface of the proximal portion of the shaft is a slight ridge, the *deltoid ridge*. At the distal end are two articular surfaces, one large and pulley-like—*trochlea*—for the ulna; the other smaller—*capitellum*—for the radius: laterally are two prominences or *condyles*, an internal and an external.

The radius and ulna are firmly fixed together so as to be incapable of movement, but not actually ankylosed. The radius articulates proximally with the humerus, distally with the scaphoid and lunar bones of the carpus. The ulna presents on the anterior aspect of its proximal end a deep fossa, the *greater sigmoid cavity*, for the trochlea of the humerus; the prominent process on the proximal side of this is the *olecranon* process. Distally it articulates with the cuneiform.



FIG. 1021.—**Lepus cuniculus.** Distal end of fore-arm and carpus, dorsal view, the bones bent towards the dorsal side so as to be partly separated. *cent.* centrale; *cun.* cuneiform; *lun.* lunar; *mag.* magnum; *rad.* radius; *sc.* scaphoid; *trpz.* trapezoid; *trpm.* trapezium; *uln.* ulna; *unc.* unciform; *I—V*, bases of metacarpals. (After Krause.)

The carpal bones (Fig. 1021), nine in number, are all small bones of irregular shape. Eight of these are arranged in two rows—a proximal and a distal; the ninth, *centrale* (*cent.*), lies between the two rows. The bones of the proximal row are—taken in order from the inner to the outer side, *scaphoid* (*sc.*), *lunar* (or *semi-lunar*) (*lun.*), *cuneiform* (*cun.*), and *pisiform*. Those of the distal row are, reckoned in the same order, *trapezium* (*trpm.*), *trapezoid* (*trpz.*), *magnum* (*mag.*), and *unciform* (*unc.*)[1]

The five metacarpals are all small, but relatively narrow and elongated, bones, the first being smaller than the rest. Each of the five digits has three phalanges, except the first, which has only two. The distal (ungual) phalanges are grooved dorsally for the attachment of the horny claw.

[1] The homologies of these bones are not quite certain, but are very probably as follows:—scaphoid = radiale, lunar = 1st centrale, cuneiform = intermedium, pisiform = ulnare, centrale = 2nd centrale, trapezium = 1st distale, trapezoid = 2nd distale, magnum = 3rd distale, unciform = 4th and 5th distalia.

The pelvic arch (Fig. 1022) contains the same elements as in the Pigeon, but the union of the ilium with the sacrum is less intimate, the acetabulum is not perforated, and the pubes of opposite sides unite ventrally in a symphysis (*sy.*). The three bones of the pelvis, ilium, pubis and ischium, are separate ossifications in the young Rabbit; but in an adult animal complete fusion takes place between the bones. The ilium and ischium meet in the acetabulum or articular cavity, which they contribute to form for the head of the femur, but the remainder of the cavity is bounded, not by the pubis, but by a small intercalated ossification—the *cotyloid* bone. The ilium (*il.*) has a rough surface for articulation with the sacrum. Between the pubis (*pub.*) in front and the ischium (*isch.*) behind is a large aperture—the *obturator foramen* (*obt.*). The femur is rotated forwards when compared with that of the Lizard, so that the limb is nearly in the same plane as the fore-limb, and the pre-axial border is internal and the originally dorsal surface anterior. The femur has at its proximal end a prominent *head* for articulation with the acetabulum, external to this a prominent process—the *great trochanter*, and internally a much smaller—the *lesser trochanter*, while a small process or *third trochanter* is situated on the outer border a little below the great trochanter. At its distal end are two prominences or *condyles*, with a depression between them. Two small sesamoids or *fabellæ* are situated opposite the distal end on its posterior aspect; and opposite the knee-joint, or articulation between the femur and the tibia, is a larger bone of similar character—the *patella*. The tibia has at its proximal end two articular surfaces for the condyles of the femur; distally it has also two articular surfaces, one, internal, for the astragalus, the other for the calcaneum. The fibula is a slender bone which becomes complétely fused distally with the tibia.

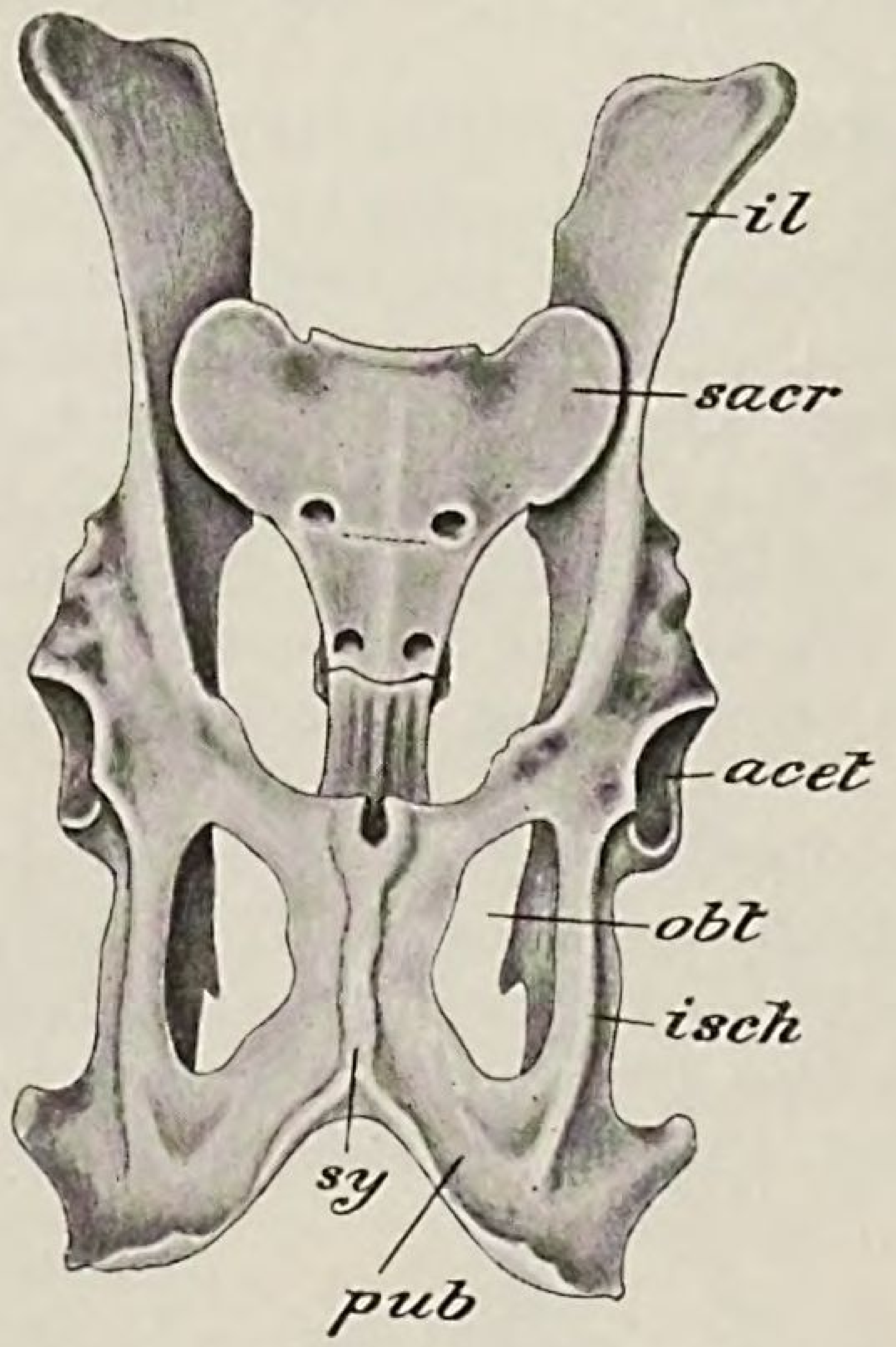


FIG. 1022.—**Lepus cuniculus.** Innominate bones and sacrum, ventral aspect. *acet.* acetabulum; *il.* ilium; *isch.* ischium; *obt* obturator foramen; *pub.* pubis; *sacr.* sacrum; *sy.* symphysis.

The tarsus (Fig. 1023) consists of six bones of irregular shape, arranged in two rows, one of the bones—the *navicular* (*nav.*)—being intercalated between the two rows. In the proximal row are two bones—the *astragalus* (*ast.*) and the *calcaneum* (*cal.*)—both articulating with the tibia; the calcaneum presents behind a long

calcaneal process. The distal row contains three bones the *meso-cuneiform*, *ectocuneiform* and *cuboid* (*cub.*); the *ento-cuneiform*, which commonly forms the most internal member of this row in other Mammals, is not present as a separate bone.[1]

There are four metatarsals, the hallux or first digit being absent. The proximal end of the second is produced into a process which articulates with the navicular. Each of the digits has three phalanges, which are similar in character to those of the manus.

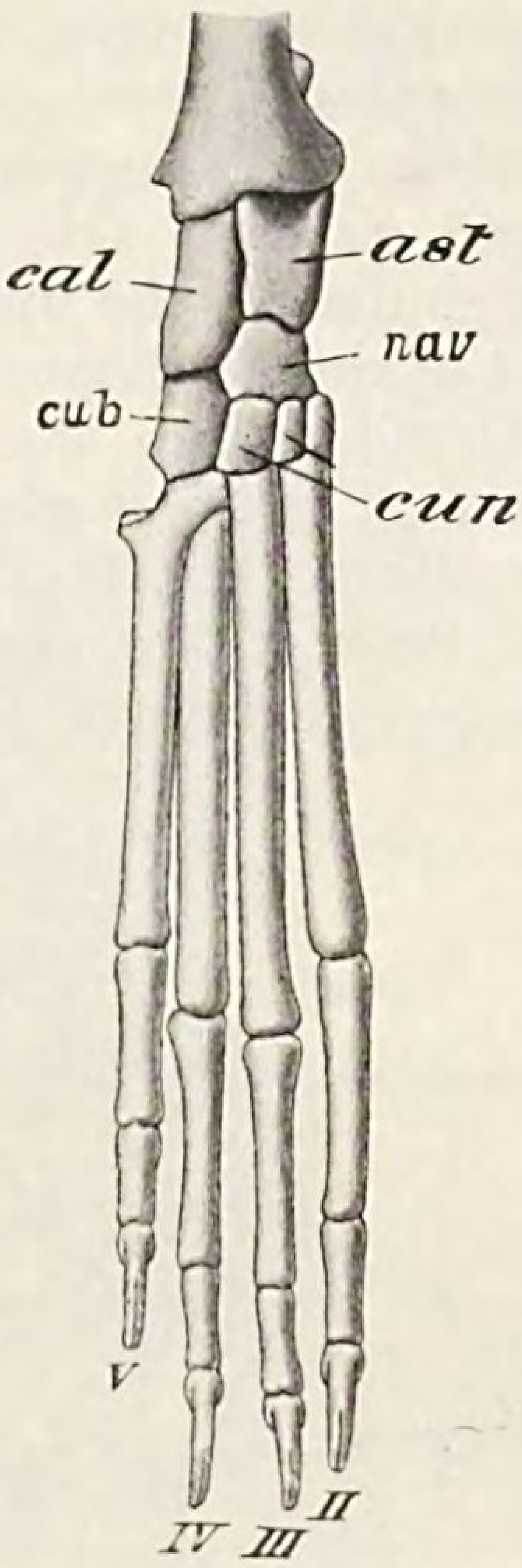


FIG. 1023.—**Lepus cuniculus.** Skeleton of pes. *ast.* astragalus; *cal.* calcaneum; *cub.* cuboid; *cun.* cuneiforms; *nav.* navicular.

The **cœlome** of the Rabbit differs from that of the Pigeon and Lizard in being divided into two parts by a dorso-ventral muscular partition, the *diaphragm.* The anterior part, or *thorax,* contains the heart and the roots of the great vessels, the lungs and bronchi, and the posterior part of the œsophagus. The posterior part, or *abdomen*, contains the stomach and intestine, the liver and pancreas, the spleen, the kidneys, ureters and urinary bladder, and the organs of reproduction.

Digestive Organs.—The teeth (Fig. 1019) are lodged in sockets or *alveoli* in the pre-maxillæ, the maxillæ, and the mandible. In the pre-maxillæ are situated four teeth—the four *upper incisors.* Of these the two anterior are very long, curved, chisel-shaped teeth, which are devoid of roots, growing throughout life from persistent pulps. Enamel is present as a thick layer on the anterior convex surface only, which accounts for the bevelled-off character of the distal end—the layer of enamel being much harder than the rest, which therefore wears more quickly away at the cutting extremity of the tooth. Along the anterior surface is a longitudinal groove. The second pair of incisors of the upper jaw are small teeth which are lodged just behind the larger pair. In the lower jaw are two incisors, which correspond in shape with the anterior pair of the upper jaw, the main difference consisting in the absence of the longitudinal groove. The remaining teeth of the upper jaw are lodged in the maxillæ. *Canines*, present in most Mammals as a single tooth on each side,

[1] In all probability the homologies of these bones are as follows:—astragalus = tibiale + intermedium, calcaneum = fibulare, navicular = centrale, ento-cuneiform = 1st distale, meso-cuneiform = 2nd distale, ecto-cuneiform = 3rd distale, cuboid = 4th and 5th distalia.

are here entirely absent, and there is a considerable space, or *diastema,* as it is termed, between the incisors and the teeth next in order—the *pre-molars.* Of these there are three in the upper jaw and two in the lower. They are long, curved teeth devoid of fangs, the first smaller than the others and of simple shape, the rest grooved longitudinally on the outer side and with two transverse grooves, bounded by ridges, on their crowns. The first pre-molar of the lower jaw has two grooves and three ridges; the second is similar to those of the upper jaw. Behind the pre-molars are the *molars,* three on each side both in the upper and lower jaws. These are similar to the upper pre-molars, except the last, which is small and of simple shape.

Opening into the cavity of the mouth are the ducts of four pairs of salivary glands—the *parotid,* the *infraorbital,* the *submaxillary* (Fig. 1025, *s. mx. gl.*), and the *sublingual* (*s. gl.*). On the floor of the mouth is the muscular tongue, covered with a mucous membrane which is beset with many papillæ. The roof of the mouth is formed by the *palate.* The anterior part, or *hard palate,* is crossed by a series of transverse ridges of its mucous membrane. The posterior part, or *soft palate,* ends behind in a free pendulous flap in front of the opening of the *posterior nares.* At the anterior end of the palate is a pair of openings—the *naso-palatine* canals or *anterior palatine canals,* leading into a pair of tubular structures—the *organs of Jacobson* (Fig. 1024, *jcb.*)—enclosed in cartilage and situated on the floor of the nasal cavities. Behind the mouth or buccal cavity proper is the *pharynx.* The pharynx is divided into two parts, an upper or *nasal* division, and a lower or *buccal* division, by the soft palate. Into the nasal division open in front the two posterior nares, and at the sides the openings of the



FIG. 1024.—**Lepus cuniculus.** Vertical section through the anterior part of the nasal region of the head. *inc.* section of larger incisor tooth; *jcb.* lumen of Jacobson's organ, surrounded by cartilage; *lcr. dct.* lacrymal duct; *max.* maxilla; *max. trb.* maxillary turbinals; *nas.* nasal bone; *nas. pal.* naso-palatine canal; *sept. cart.* cartilaginous nasal septum. (After Krause.)

Eustachian tubes. The nasal division is continuous with the buccal division round the posterior free edge of the soft palate. From the buccal division leads ventrally the slit-like opening of the glottis[1] into the larynx and trachea; overhanging the glottis is a leaf-like movable flap (Fig. 1025, *ep.*) formed of a plate of yellow elastic cartilage covered with mucous membrane; this is the *epiglottis.* Behind the pharynx becomes continuous with the *œsophagus* or gullet (*œs.*). The latter is a narrow but dilatable muscular tube, which runs backwards from the pharynx through

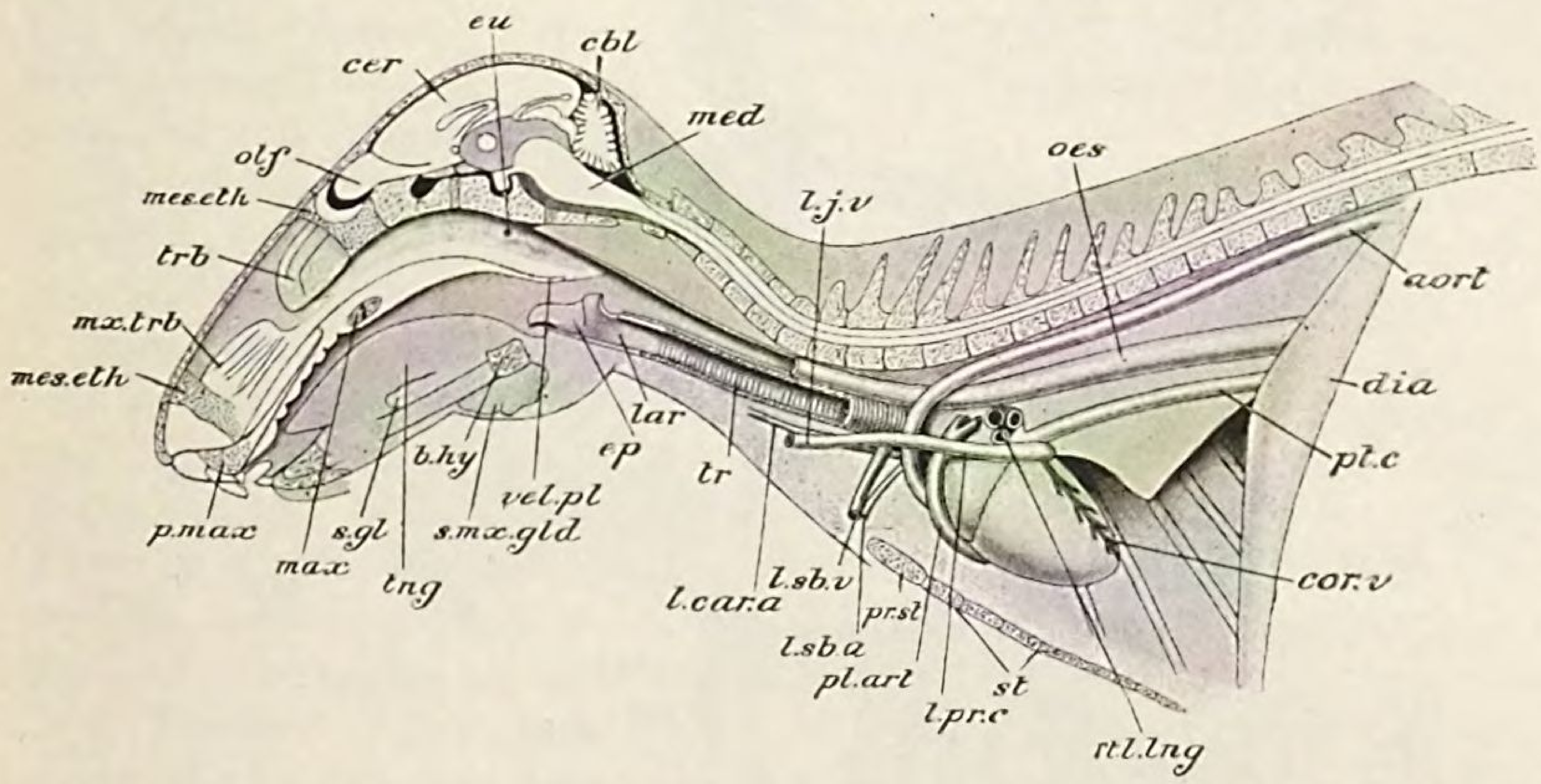


FIG. 1025.—**Lepus cuniculus.** Lateral dissection of the head, neck and thorax. The head and spinal column are represented in mesial vertical section; the left lung is removed; the greater part of the nasal septum is removed so as to show the right nasal cavity with its turbinals. *aort.* dorsal aorta; *b.hy.* basi-hyal; *cbl.* cerebellum; *cer.* cerebral hemispheres; *cor. v.* coronary vein; *dia.* diaphragm; *ep.* epiglottis; *eu.* opening of Eustachian tube into pharynx; *lar.* larynx; *l. j. v.* left jugular vein; *l. sb. a.* left subclavian artery; *l. sb. v.* left subclavian vein; *max.* maxilla; *med.* medulla; *mes.eth.* mesethmoid; *mx.trb.* maxilla-turbinal; *œs.* œsophagus; *olf.* olfactory lobe; *pl. a.* pulmonary artery; *p.max.* pre-maxilla; *pr.st.* presternum; *pt.c.* post-caval vein; *rt.lng.* root of left lung with bronchus and pulmonary veins and artery cut across; *s. gl.* sub-lingual salivary gland; *s.mx. gl.* sub-maxillary salivary gland; *st.* sternebræ; *tng.* tongue *tr* trachea; *trb.* ethmo-turbinals; *vel. pl.* soft palate.

the neck and thorax to enter the cavity of the abdomen through an aperture in the diaphragm, and opens into the *stomach.*

The stomach (Fig. 1026) is a wide sac, much wider at the end (*cardiac*), at which the œsophagus enters, than at the opposite or *pyloric* end, where it passes into the small intestine. The small intestine is an elongated, narrow, greatly coiled tube, the first part of which, or *duodenum* (*du* and *du'*), forms a U-shaped loop. The large intestine is a wide tube, the first and greater part of which, termed the *colon,* has its walls sacculated, a structure which is absent in the short, straight posterior part or *rectum* (*rct.*). At the junction of the small with the large intestine is a very wide blind tube, the *cæcum,* which is of considerable length and is

[1] The term glottis is more strictly applied not to this slit, but to the entire passage from the pharynx to the trachea.

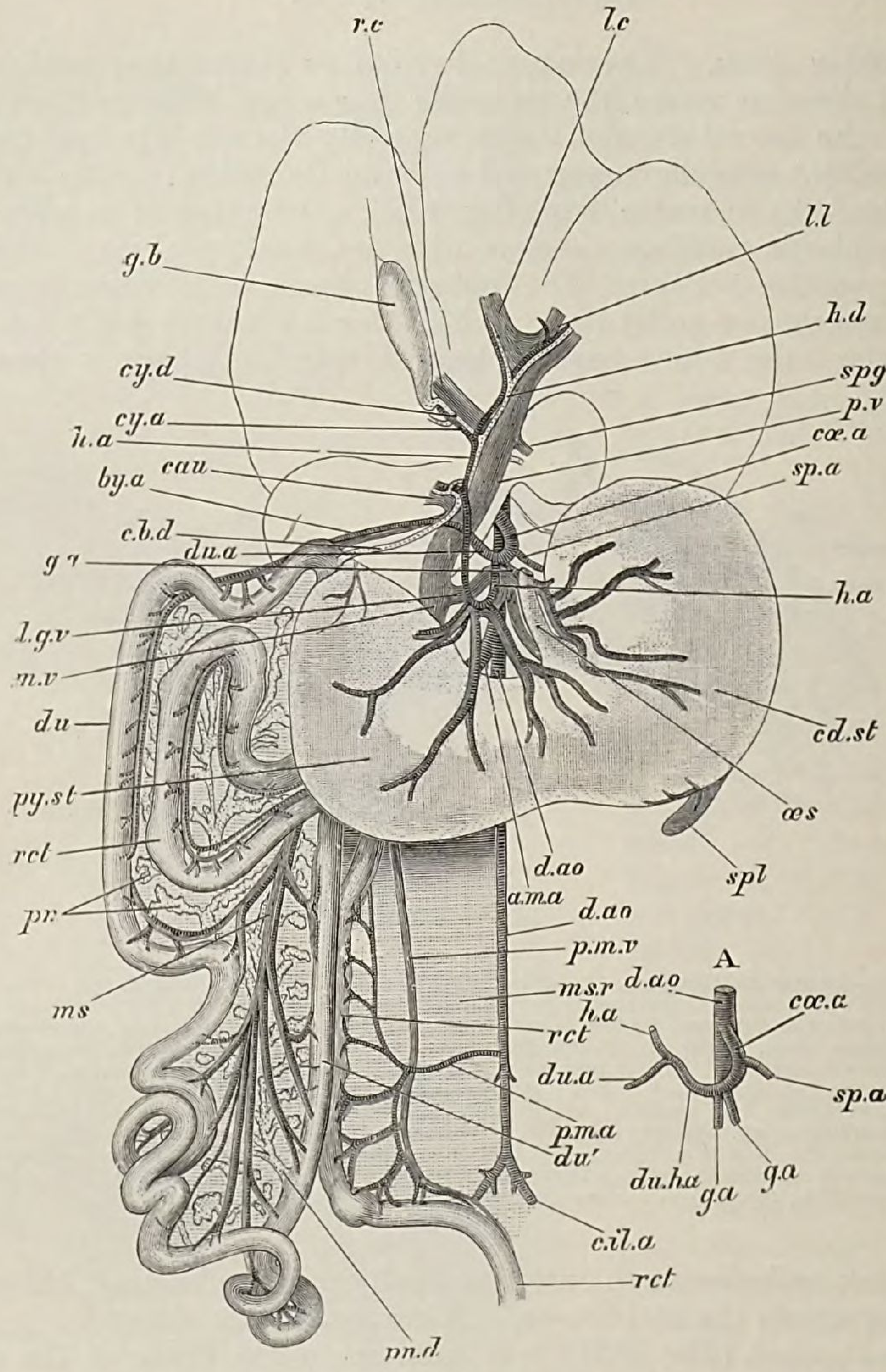


Fig. 1026.—**Lepus cuniculus.** The stomach, duodenum, posterior portion of rectum and liver (in outline) with their arteries, veins and ducts. *A*, the cœliac artery of another specimen (both × $\frac{2}{3}$). The gullet is cut through and the stomach somewhat displaced backwards to show the ramifications of the cœliac artery (*cœ. a.*); the duodenum is spread out to the right of the subject to show the pancreas (*pn.*); the branches of the bile-duct (*c. b. d.*) portal vein (*p. v.*) and hepatic artery (*h. a.*) are supposed to be traced some distance into the various lobes of the liver. *a. m. a.* anterior mesenteric artery; *cau.* caudate lobe of liver with its artery, vein and bile-duct; *c. b. d.* common bile-duct; *cd. st.* cardiac portion of stomach; *c. il. a.* common iliac artery; *cœ. a.* cœliac artery; *cy. a.* cystic artery; *cy. d.* cystic duct; *d. ao.* dorsal aorta; *du.* proximal, and *du'*, distal limbs of duodenum; *du. a.* duodenal artery; *du. h.a.* (in *A*), duodeno-hepatic artery; *g. a.* gastric artery and vein; *g. b.* gall bladder; *h. a.* hepatic artery; *b. d.* left bile-duct; *l. c.* left central lobe of liver, with its artery, vein and bile-duct; *l. g. v.* lieno-gastric vein; *l. l.* left lateral lobe of liver with its artery, vein and bile-duct; *ms.* branch of mesenteric artery and vein to duodenum; *ms.r.* meso-rectum; *m. v.* chief mesenteric vein; *œs.* œsophagus; *p. m. a.* posterior mesenteric artery; *p. m. v.* posterior mesenteric vein; *pn.* pancreas; *pn. d.* pancreatic duct; *p. v.* portal vein; *py. st.* pyloric portion of stomach; *rct.* rectum; *r. c.* right central lobe of liver, with artery, vein and bile-duct; *spg.* Spigelian lobe of liver with its artery, vein and bile-duct *spl.* spleen *sp. a.* splenic artery. (From Parker's *Zootomy*.

marked by a spiral constriction, indicating the presence in its interior of a narrow spiral valve. At its extremity is a small, fleshy, finger-like *vermiform appendix.*

The intestine, like that of the Pigeon, is attached throughout its length to the dorsal wall of the abdominal cavity by a *mesentery*, or fold of the lining membrane or peritoneum.

The *liver* is attached to the diaphragm by a fold of the peritoneum. Its substance is partly divided by a series of fissures into five lobes. A thin-walled gall-bladder lies in a depression on its posterior surface. The *common bile-duct* (*c. b. d.*) formed by the union of *cystic duct* from the gall-bladder and *hepatic ducts* from the various parts of the liver, runs to open into the duodenum near the pylorus.

The *pancreas* (*pn.*) is a diffused gland in the fold of mesentery passing across the loop of the duodenum. Its single duct, the *pancreatic duct* (*pn. d.*), opens into the distal limb of the loop.

Circulatory Organs.—The *heart* (Fig. 1027) is situated in the cavity of the thorax, a little to the left of the middle line, and lies between the two pleural sacs enclosing the lungs. Between the pleural sacs is a space, the *mediastinum* (Fig. 1030). This is divisible into four parts, the anterior, the dorsal, the middle, and the ventral. In the anterior part lie the posterior part of the trachea, the neighbouring part of the œsophagus and thoracic duct, the roots of the great arteries, and the veins of the pre-caval system, the thymus gland, and the phrenic, pneumogastric, and other nerves. In the dorsal part are situated the posterior part of the œsophagus, the thoracic part of the dorsal aorta, the pneumogastric nerve, the azygos vein, and the thoracic duct. The middle part is the widest, and lodges the heart and roots of the aorta and pulmonary artery enclosed in the pericardium, the posterior portion of the pre-caval veins, the phrenic nerves, the terminal part of the azygos vein, and the roots of the lungs. The ventral part contains only areolar tissue with the lymphatic glands. The pericardial membrane enclosing the heart consists of two layers, a *parietal*, forming the wall of the pericardial cavity, and a *visceral*, immediately investing the heart. Between the two is a narrow cavity containing a little fluid—the *pericardial fluid.* In general shape the heart resembles the heart of the Pigeon, with the apex directed backwards and slightly to the left, and the base forwards. Like that of the Pigeon, it contains right and left auricles and right and left ventricles, the right and left sides of the heart having their cavities completely separated off from one another by inter-auricular and inter-ventricular partitions.

Into the right auricle open three large veins—the *right* and *left pre-caval* veins and the single *post-caval*—the first into the anterior part, the second into the left-hand side of the posterior portion, and the third into the dorsal surface. Projecting forwards from it

is an ear-like *auricular appendix,* the inner surface of which is raised up into numerous cords of muscular fibres, the *musculi pectinati.* A membranous fold, the remnant of the fœtal *Eustachian valve,* extends from the opening of the post-caval forwards towards the auricular septum. The opening of the left pre-caval is bounded behind by a crescentic fold, the *valve of Thebesius.* On the septum is an oval area where the partition is thinner than elsewhere; this is the *fossa ovalis* (*f. ov.*); it marks the position of an aperture, the *foramen ovale,* in the fœtus. The crescentic upper rim of the aperture is known as the *annulus ovalis.* The cavity of the right auricle communicates with that of the right ventricle by the wide right auriculo-ventricular opening. This is guarded by a valve, the *tricuspid* (*tri. v.*), composed of three membranous lobes or cusps, so arranged and attached that while they flap back against the walls of the ventricle to allow the passage of blood from the auricle to the ventricle, they meet together across the aperture so as to close the passage when the ventricle contracts. The lobes of the valve are attached to muscular processes of the wall of the ventricle, the *musculi papillares* (*m. pap.*), by means of tendinous threads called the *chordæ tendineæ.* The right ventricle, much thicker than the auricle, forms the right side of the conical apical portion, but does not extend quite to the apex. Its walls are raised up into muscular ridges called *columnæ carneæ.* It gives off in front, at its left anterior angle, the pulmonary artery, the entrance to which is guarded by three pouch-like *semi-lunar valves* (*sem. v.*).

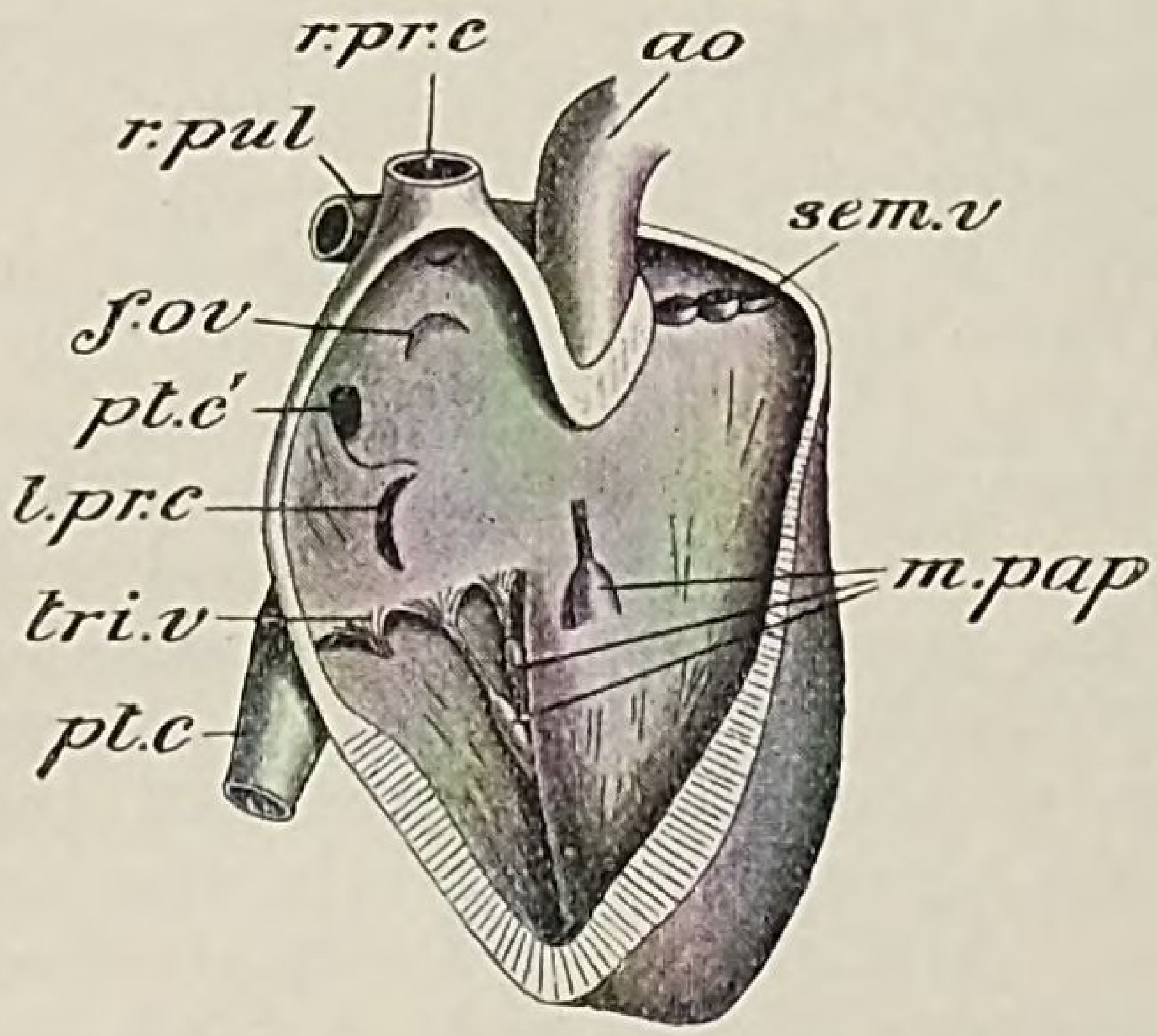


FIG. 1027.—**Lepus cuniculus.** Heart, seen from the right side, the walls of the right auricle and right ventricle partly removed so as to expose the cavities. *ao.* aorta; *f. ov.* fossa ovalis; *l. pr. c.* opening of left pre-caval; *m. pap.* musculi papillares; *pt. c.* post-caval; *pt. c'.* opening of post-caval; *r. pr. c.* right pre-caval; *r. pul.* right pulmonary artery; *sem. v.* semi-lunar valves; *tri. v.* tricuspid valve.

The left auricle, like the right, is provided with an auricular appendix. Into its cavity on its dorsal aspect open together the right and left pulmonary veins. A large left auriculo-ventricular opening leads from the cavity of the left auricle into that of the left ventricle: this is guarded by a valve, the *mitral,* consisting of two membranous lobes or cusps with chordæ tendineæ and musculi papillares. In the walls of the ventricle are columnæ carneæ rather more strongly developed than in the right. At the basal (anterior) end of the left ventricle is the opening of the aorta, guarded by

three semi-lunar valves similar to those at the entrance of the pulmonary artery. The *coronary* arteries, which supply the muscular substance of the heart, are given off from the aorta just beyond the semi-lunar valves. The corresponding vein opens into the terminal part of the left pre-caval. The pulmonary artery divides into two, a right and a left, each going to the corresponding lung.

The aorta gives origin to a system of arterial trunks by which the arterial blood is conveyed throughout the body. It first runs forwards from the base of the left ventricle, then bends round the left bronchus, forming the *arch* of the aorta (Fig. 1028, *a. ao.*), to run backwards through the thorax and abdomen, in close contact with the spinal column, as the *dorsal aorta* (*d. ao.*). From the arch of the aorta are given off two large arteries, the *innominate* (*in.*) and the *left subclavian.* The innominate divides to form the *right subclavian* (*s. cla.*) and the *right* (*r. c. c.*) and *left* (*l. c. c.*) *carotid* arteries. The right subclavian passes to the fore-limb as the *brachial* artery, giving origin first to the *vertebral* artery, which, after passing up through the vertebrarterial canal, enters the cranial cavity, having first supplied branches to the spinal cord, and then to the *internal mammary,* which supplies the side of the chest behind the root of the fore-limb. The right carotid divides opposite the angle of the jaw into *internal* and *external carotids.* The left carotid and left subclavian correspond in their distribution and branching to the right carotid and right subclavian respectively. The aorta, in passing through the thorax, gives off a series of small paired *inter-costal* arteries (*i. cs.*). In the abdomen its first large branch is the *cœliac artery* (*cœ.*), which supplies the liver, stomach, and spleen. Behind this it gives origin to the *anterior mesenteric* (*a. m.*), which supplies the intestine and the pancreas. Opposite the kidneys it gives off the two renal arteries (*r.*) for the supply of these organs, and a good deal further back the *spermatic* (*spm.*) or *ovarian* arteries for the testes or ovaries, as the case may be. Just in front of the origin of the spermatic arteries is given off a *posterior mesenteric* (*p. m.*), which supplies the hinder part of the rectum. A series of small *lumbar* arteries supply the side-walls of the abdominal cavity. Posteriorly the dorsal aorta divides to form the two common iliac arteries (*c. il. a.*) which supply the hind-limb, a small *median sacral* (*caudal*) artery (*ms. c.*) passing backwards in the middle line to supply the caudal region.

The system of *caval* veins which open into the right auricle consists of the *right* and *left pre-cavals* and of the single *post-caval.* The right pre-caval is formed by the union of the *right jugular* (*e. ju.*) vein and *right subclavian* (*scl. v.*). The *vena azygos* (*az. v.*), the *right anterior intercostal* (*i. cs.*), and the *right internal mammary* also open into it. The left pre-caval receives a series of

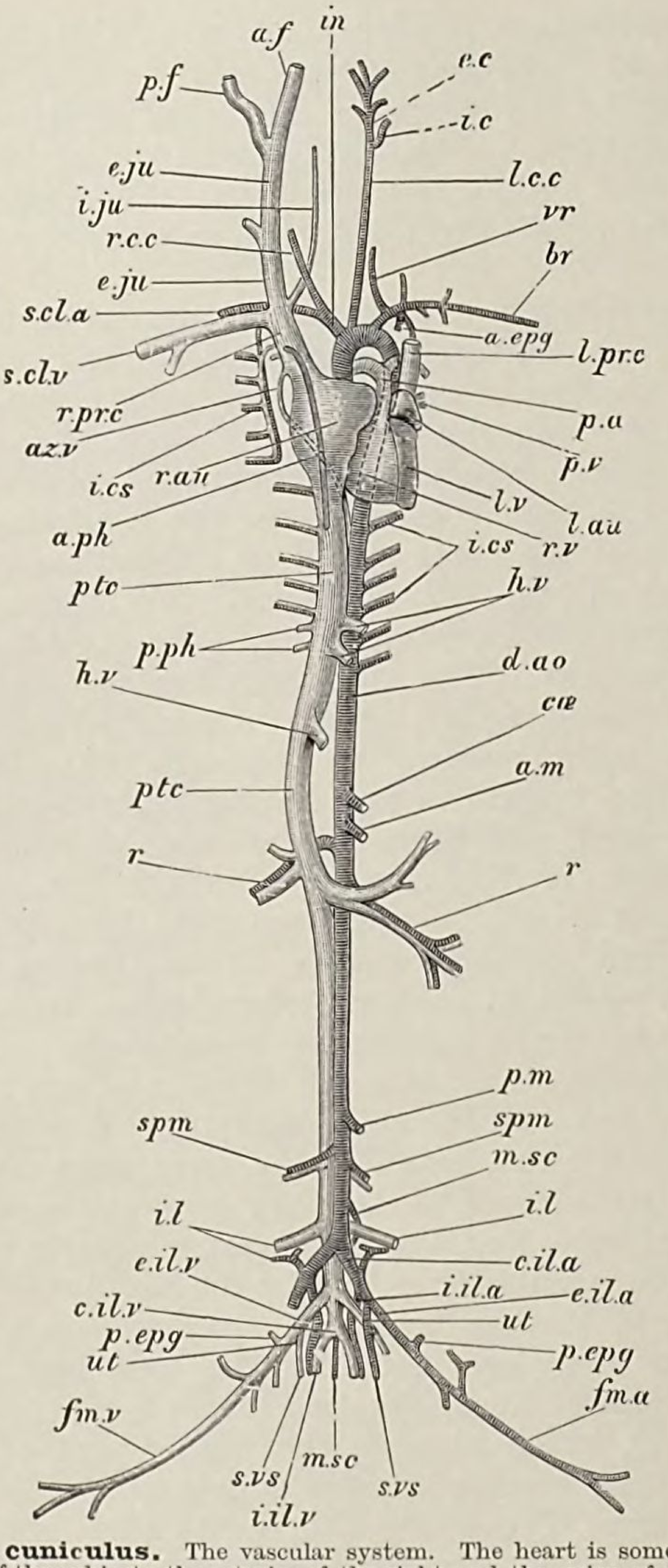


FIG. 1028.—**Lepus cuniculus.** The vascular system. The heart is somewhat displaced towards the left of the subject; the arteries of the right and the veins of the left side are in great measure removed. *a. ao.* arch of the aorta; *a. epg*, internal mammary artery; *a. f.* anterior facial vein; *a. m.* anterior mesenteric artery; *a. ph.* anterior phrenic vein; *az. v.* azygos vein; *br.* brachial artery; *c. il. a.* common iliac artery; *cœ.* cœliac artery; *d. ao.* dorsal aorta; *e. c.* external carotid artery; *e. il. a.* external iliac artery; *e. il. v.* external iliac vein; *e. ju.* external jugular vein; *fm. a.* femoral artery; *fm. v.* femoral vein; *h. v.* hepatic veins; *i. c.* internal carotid artery; *i. cs.* intercostal vessels; *i. ju.* internal jugular vein; *i.l.* ilio-lumbar artery and vein; *in.* innominate artery; *l. au.* left auricle; *l. c. c.* left common carotid artery; *l. prc.* left pre-caval vein; *l. v.* left ventricle; *m. sc.* median sacral artery; *p. a.* pulmonary artery; *p. epg.* epigastric artery and vein; *p. f.* posterior facial vein; *p. m.* posterior mesenteric artery; *p. ph.* posterior phrenic veins; *ptc.* post-caval veins; *p. v.* pulmonary vein; *r.* renal artery and vein; *r. au.* right auricle; *r. c. c.* right common carotid artery; *r. prc.* right pre-caval vein; *r. v.* right ventricle; *scl. a.* right sub-clavian artery; *scl. v.* sub-clavian vein; *spm.* spermatic artery and vein; *s. vs.* superior vesical artery and vein; *ut.* uterine artery and vein; *vr.* vertebral artery. (From Parker's *Zootomy.*)

veins similar to those forming the right, except that it has no azygos branch.

The post-caval vein (*pt. c.*) is formed in the hinder part of the abdominal cavity by the union of the *internal iliacs* (*i. il. v.*) bringing the blood from the back of the thighs. Shortly after its origin it receives the two *external iliacs* (*e. il. v.*) bringing the blood from the hind-limb. In front of this a pair of *ilio-lumbar* (*i.l.*) veins join it; a little farther forward a pair of *spermatic* (*spm.*) (in the male) or *ovarian* (in the female) veins; and opposite the kidneys a pair of *renal* veins (*r.*). From the liver the blood is carried to the post-caval by the *hepatic* veins. A pair of small *posterior phrenic* veins (*p. ph.*) bring the blood from the diaphragm and open into the post-caval as it passes through the substance of the latter.

The *hepatic portal system* consists, as in other Vertebrates, of a system of veins conveying blood from the various parts of the alimentary canal to the liver, the trunks of the system uniting to form the single large *portal vein* (Fig. 1026, *p. v.*). The principal veins of the portal system are the *lieno-gastric*, *duodenal*, *anterior mesenteric*, and *posterior mesenteric*. There is no trace of a renal portal system. The red blood corpuscles are circular, bi-concave, non-nucleated discs.

Respiratory Organs.—The *larynx* (Fig. 1029) is a chamber with walls supported by cartilage, lying below and somewhat behind the pharynx, with which it communicates through a slit-like aperture. The cartilages of the larynx are, in addition to the *epiglottis*, which has been already referred to (p. 431), the large *thyroid* (*th.*), which forms the anterior wall, the ring-like *cricoid* (*cr.*), the two small *arytenoids* (*ary.*), and a pair of small nodules, the *cartilages of Santorini* (*sant.*), situated at the apices of the arytenoids. The *vocal cords* extend across the cavity from the thyroid in front to the arytenoids behind. Leading backwards from the larynx is the *trachea* or wind-pipe (Fig. 1025, *tr.*), a long tube the wall of which is supported by cartilaginous rings which are incomplete dorsally. The trachea enters the cavity of the thorax, and there divides into the two *bronchi*, one passing to the root of each lung.

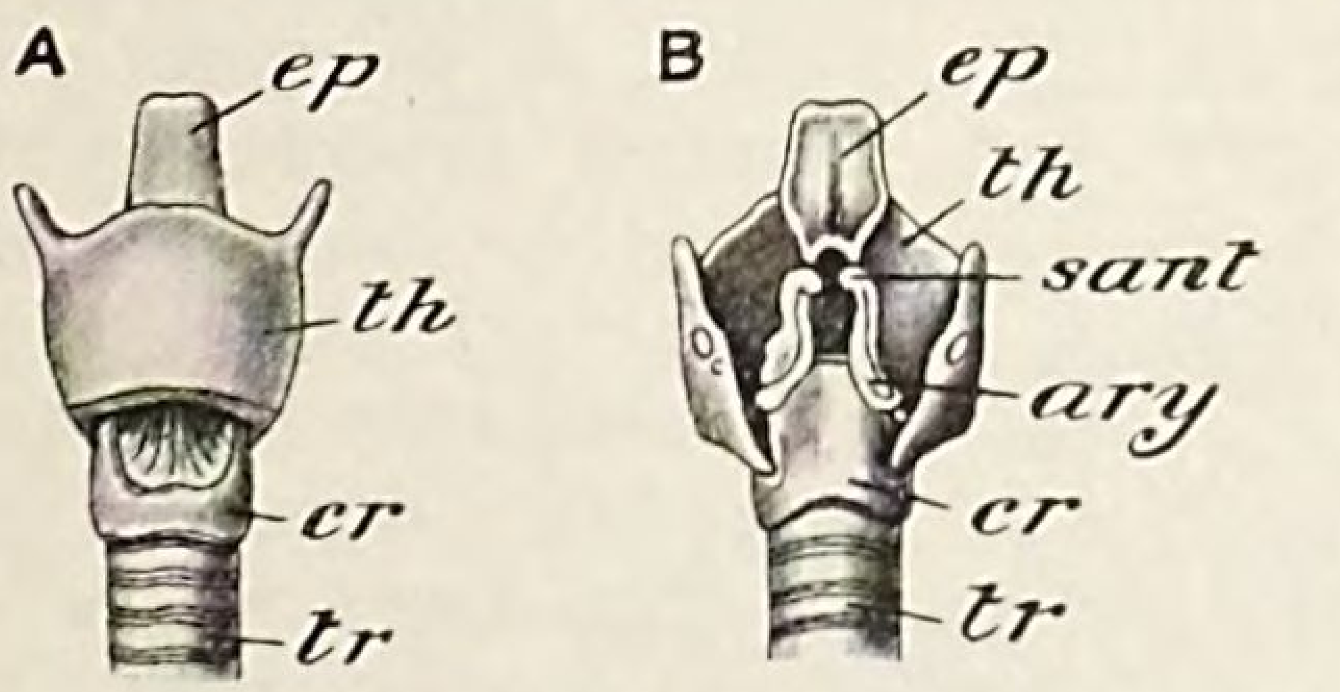


FIG. 1029.—**Lepus cuniculus.** Larynx. *A*, ventral view; *B*, dorsal view. *ary.* arytenoid; *cr.* cricoid; *ep.* epiglottis; *sant.* cartilage of Santorini; *th.* thyroid; *tr.* trachea. (From Krause, after Schneider.)

The *lungs* (Fig. 1030) are enclosed in the lateral parts of the cavity of the thorax. Each lung lies in a cavity lined by a membrane—the cavity of the *pleural sac* or *pleural membrane*. The right and left pleural sacs are separated by a considerable

interval owing to the development in the partition between them of a space, the mediastinum, in which, as already explained, lie the heart and other organs. The lung is attached only at its root, where the pleural membrane is reflected over it. In this respect it differs widely from the lung of the bird. It differs also in its minute structure. The bronchus, entering at the root, divides and subdivides to form a ramifying system of tubes each of the ultimate branches of which, or *terminal bronchioles,* opens into a minute chamber or *infundibulum*, consisting of a central passage and a number of thin-walled *air-vesicles* or *alveoli* given off from it. A group of these infundibula, supplied by a single bronchiole, which divides within it to form the terminal bronchioles, is termed a *lobule* of the lung.

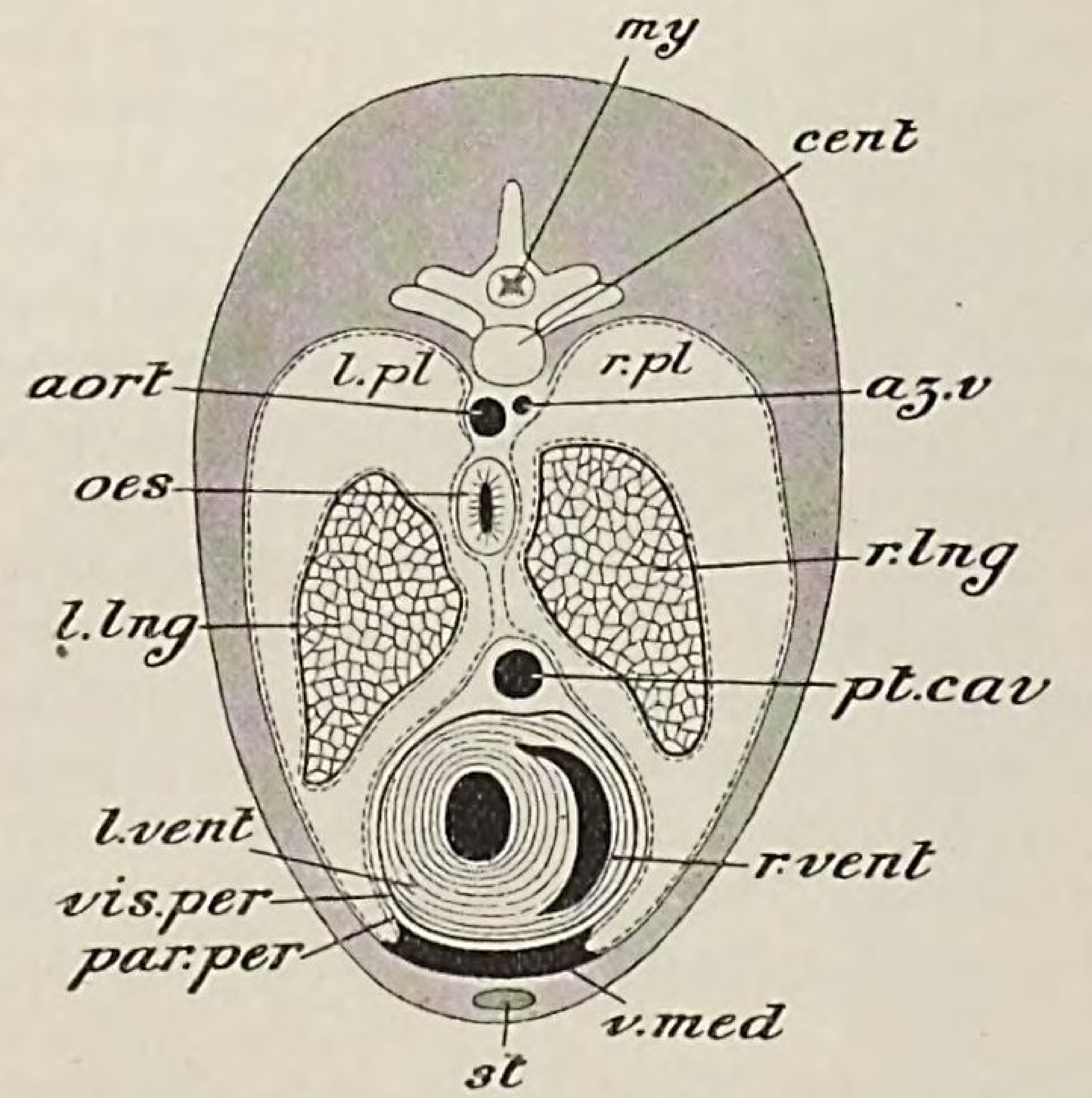


FIG. 1030.—**Lepus cuniculus.** Diagram of a transverse section of the thorax in the region of the ventricles to show the relations of the pleuræ, mediastinum, etc. The lungs are contracted. *aort.* dorsal aorta; *az. v.* azygos vein; *cent.* centrum of thoracic vertebra; *l. lng.* left lung; *l. pl.* left pleural sac; *l. vent.* left ventricle; *my.* spinal cord; *œs.* œsophagus; *pt.cav.* post-caval, close to its entrance into right auricle; *r. lng.* right lung; *r. pl.* right pleural cavity; *r. vent.* right ventricle; *st.* sternum; *v. med.* ventral mediastinum.

In shape the lung may be roughly described as conical with the apex directed forwards. The base, which is concave, lies, when the lung is distended, in contact with the convex anterior surface of the diaphragm. The outer or costal surface is convex in adaptation to the form of the side-wall of the thorax; the internal surface is concave.

Ductless Glands.—The *spleen* is an elongated, compressed, dark red body situated in the abdominal cavity in close contact with the stomach, to which it is bound by a fold of the peritoneum. The *thymus,* much larger in the young Rabbit than in the adult, is a soft mass, resembling fat in appearance, situated in the ventral division of the mediastinal space below the base of the heart. The *thyroid* is a small, brownish, bilobed, glandular body situated in close contact with the ventral surface of the larynx.

Nervous System.—The neural cavity, as in the Pigeon, contains the central organs of the cerebro-spinal nervous system—the *brain* and *spinal cord.* The brain (Figs. 1031–1033) of the Rabbit contains the same principal parts as that of the Pigeon,

with certain differences, of which the following are the most important.

The surface of the cerebral hemispheres (Fig. 1031, *f. b.*, Fig. 1032, *c. h.*), which are relatively long and narrow, presents

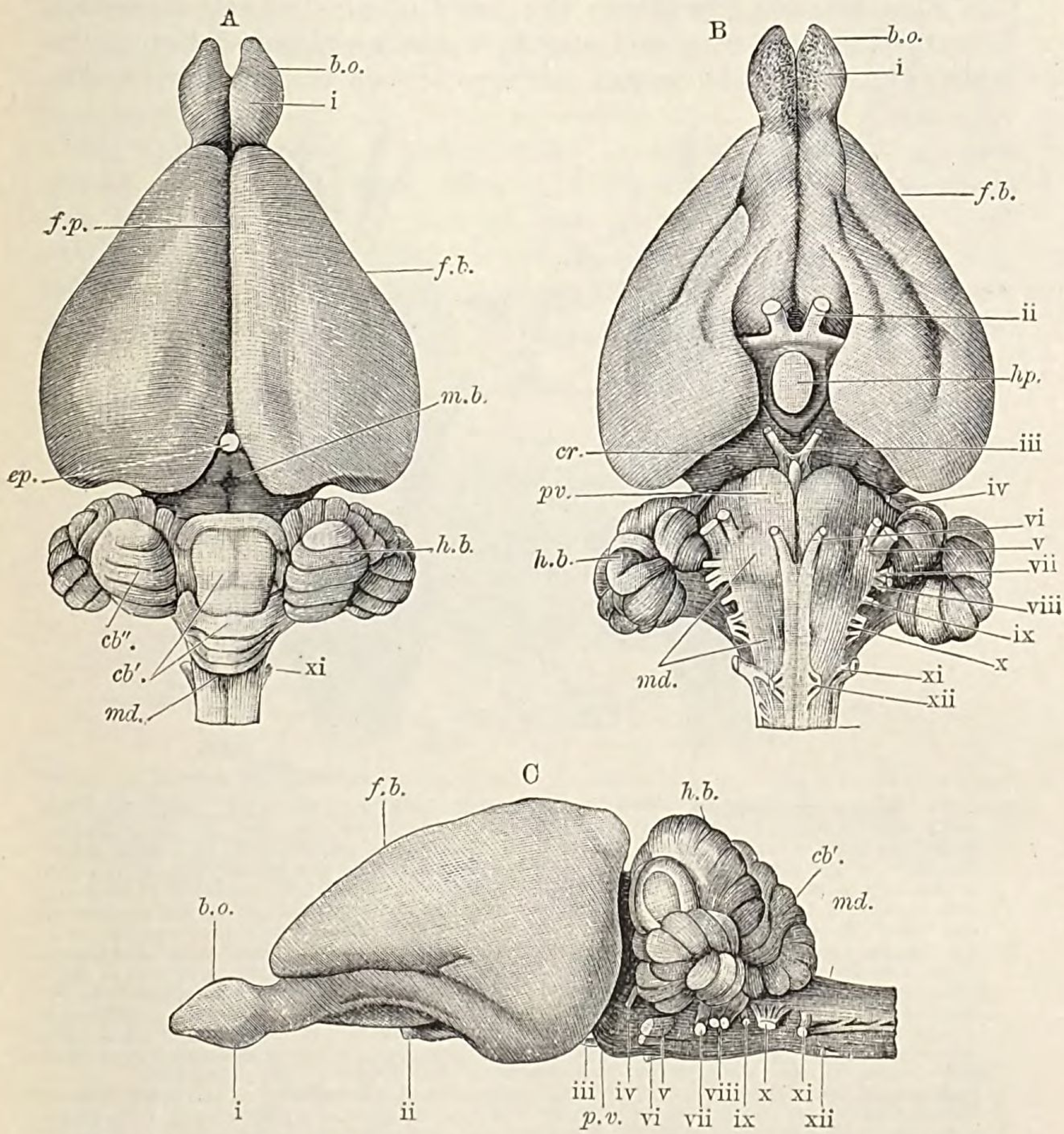


FIG. 1031.—**Lepus cuniculus.** Brain. *A*, dorsal view; *B*, ventral; *C*. lateral. *b. o.* olfactory lobe; *cb'*, median lobe of cerebellum (vermis); *cb''*. lateral lobe of cerebellum; *cr.* cauro cerebri; *ep.* epiphysis; *f,b*, parencephala; *f, p*, longitudinal fissure; *h.b.* hind-brain; *hp.* hypophysis; *m.b.* mid-brain (corpora quadrigemina); *md.* medulla oblongata; *p. v.* pons Varolii; *I—XII*, cranial nerves. (From Wiedersheim.)

certain depressions or sulci, which, though few and indistinct, yet mark out the surface into lobes or convolutions not distinguishable in the case of the Pigeon or the Lizard. A slight depression—the *Sylvian fissure*—at the side of the hemisphere separates off a lateral portion, or *temporal lobe* (Fig. 1033, *c. h*[2].),

from the rest. There are very large club-shaped olfactory lobes at the anterior extremities of the cerebral hemispheres. Connecting together the two hemispheres is a commissural structure—the *corpus callosum* (Figs. 1032, 1033, *cp. cl.*)—not present in the Pigeon; this runs transversely above the level of the lateral ventricles. Examined in transverse section, *i.e.*, in a longitudinal section of the brain (Fig. 1033), the corpus callosum is seen to bend downwards,

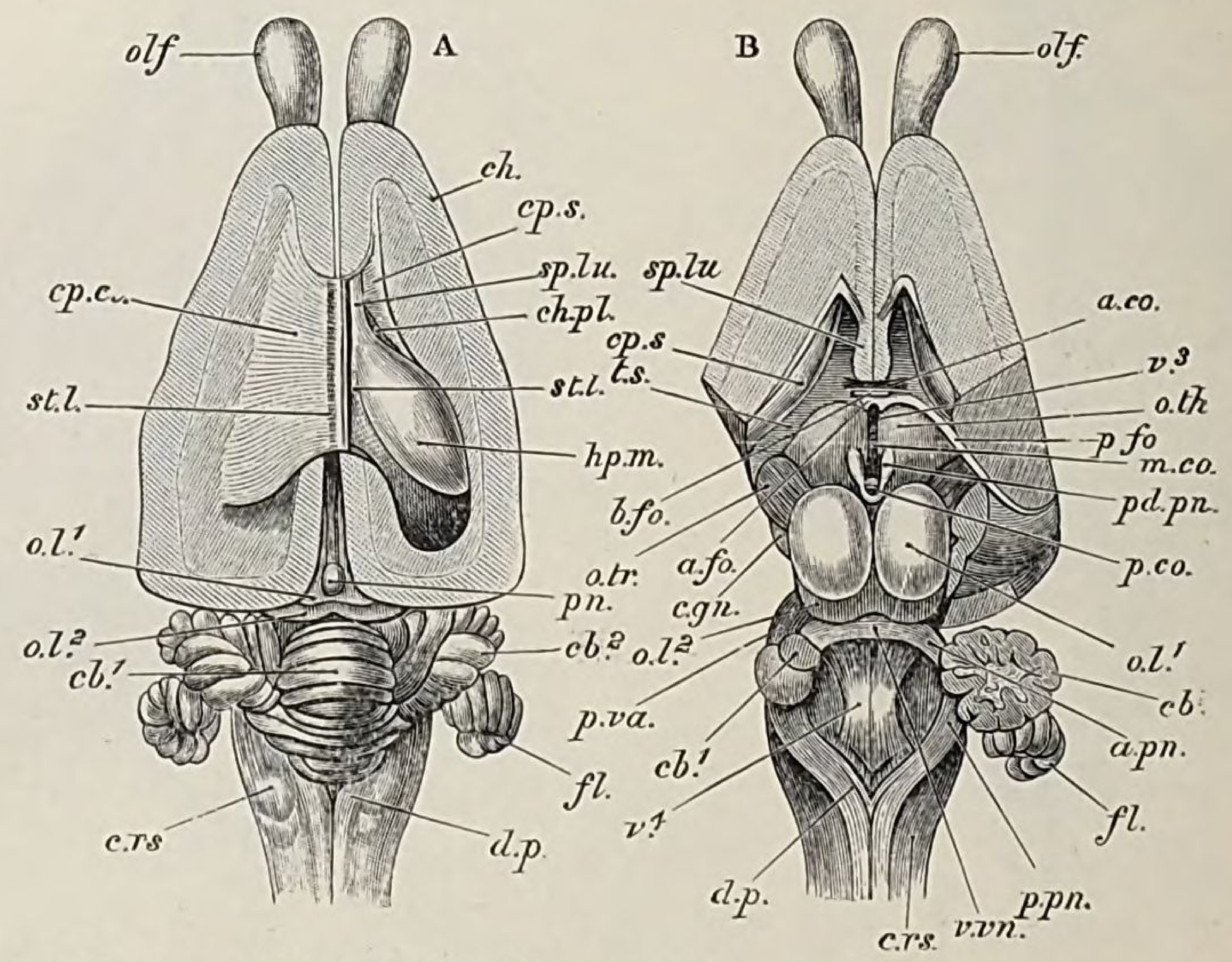


FIG. 1032.—**Lepus cuniculus.** Two dissections of the brain from above (nat. size.) In *A* the left parencephalon is dissected down to the level of the corpus callosum; on the right the lateral ventricle is exposed. In *B* the cerebral hemispheres are dissected to a little below the level of the anterior genu of the corpus callosum; only the frontal lobe of the left hemisphere is retained; of the right a portion of the temporal lobe also is left; the velum interpositum and pineal body are removed, as well as the greater part of the body of the fornix, and the whole of the left posterior pillar; the cerebellum is removed with the exception of a part of its right lateral lobe. *a. co.* anterior commissure; *a. fo.* anterior pillar of fornix; *a. pn.* anterior peduncles of cerebellum; *b. fo.* body of fornix; *cb*¹. superior vermis of cerebellum; *cb*². its lateral lobe; *c. gn.* corpus geniculatum; *c. h.* cerebral hemisphere; *ch. pl.* choroid plexus; *cp. cl.* corpus callosum; *cp. s.* corpus striatum; *c. rs.* corpus restiforme; *d. p.* dorsal pyramid; *fl.* flocculus; *hp. m.* hippocampus major; *m. co.* middle commissure; *o. l*¹. anterior; *o. l*². posterior lobes of corpora quadrigemina; *o. th.* optic thalamus; *o. tr.* optic tract; *p. co.* posterior commissure; *p. fo.* posterior pillar of fornix; *pn.* pineal body; *pd. pn.* peduncle of pineal body; *p. pn.* posterior peduncles of cerebellum; *p. va.* fibres of pons Varolii forming middle peduncles of cerebellum; *sp. lu.* septum lucidum; *st. l.* stria longitudinalis; *t. s.* tœnia semicircularis; *v. vn.* valve of Vieussens; *v*3. third ventricle; *v*4, fourth ventricle. (From Parker's *Zootomy*.)

forming what is termed the *genu*; posteriorly it bends downwards, forming the *splenium*, which passes forwards and is united with the fornix. Below the corpus callosum is another characteristic structure of a commissural nature—the *fornix* (*b. fo.*)—a narrow median strand of longitudinal fibres, which bifurcates both anteriorly and posteriorly to form the so-called *pillars* of the fornix (anterior and posterior) (*a. fo.*, *p. fo.*). Below the corpus callosum, between it and the fornix, the thin inner walls of the hemispheres (*septum*

lucidum) (*sp. lu.*) enclose a small, laterally compressed cavity, the so-called *fifth ventricle* or *pseudocœle*; this is not a true brain-ventricle, but merely a space between the closely apposed hemispheres.

The lateral ventricles of the cerebral hemispheres are much more extensively developed than in the brain of the Pigeon, and of somewhat complex shape. Each consists of a middle portion or *body* roofed over by the corpus callosum, a narrow anterior prolongation, or *anterior cornu*, a *posterior cornu*, which runs backwards and inwards, and a *descending cornu*, which passes at first almost directly outwards, then downwards, and finally inwards and forwards. On the floor of the body of the ventricle, and continued along the whole extent of the descending cornu, is a prominent ridge of nearly semicircular transverse section—the *hippocampus major* (*hp. m.*); this corresponds to a groove, the

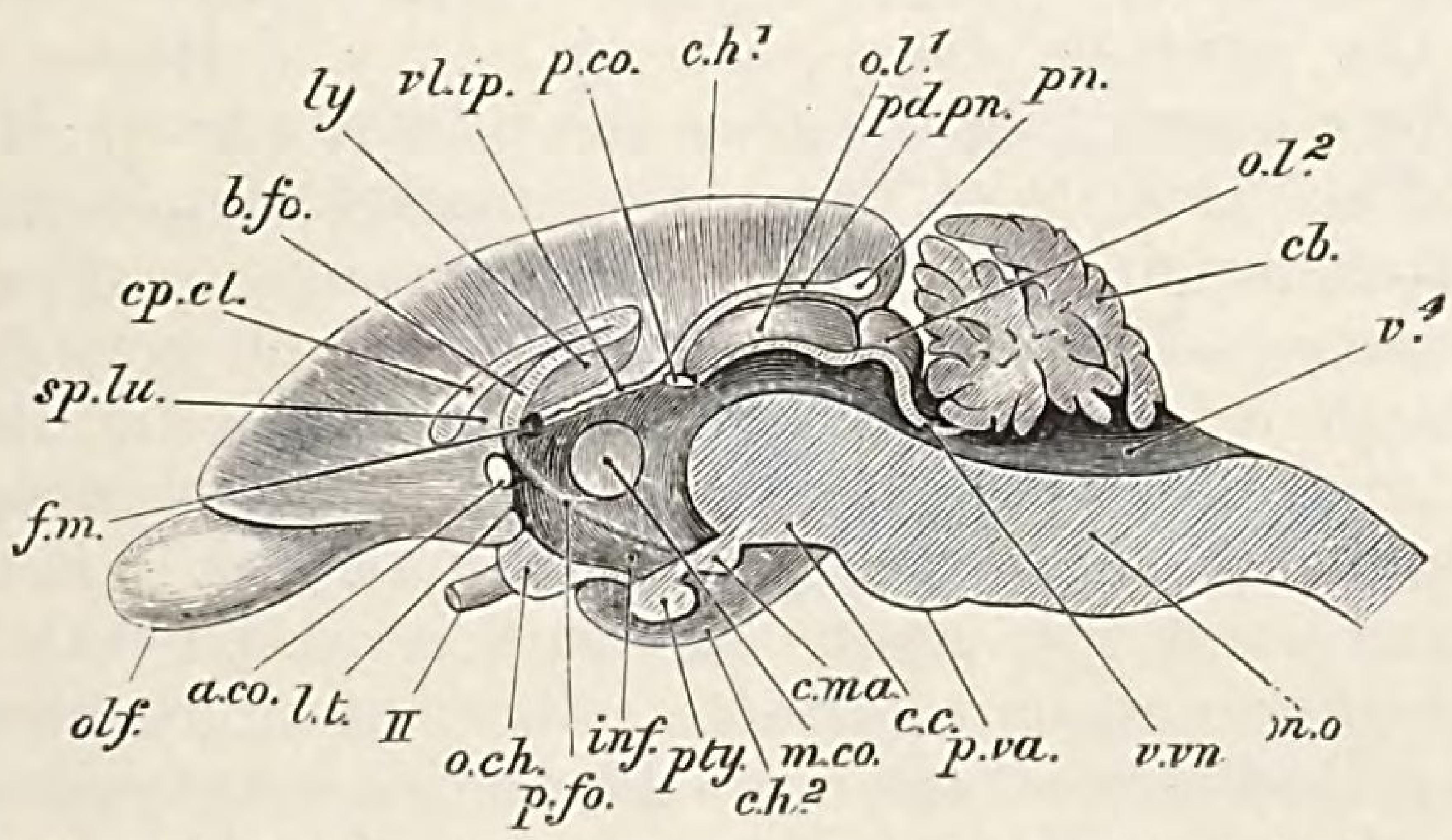


FIG. 1033.—**Lepus cuniculus.** Longitudinal vertical section of the brain (nat. size). Letters as in preceding figure; in addition, *cb.* cerebellum, showing arbor vitæ; *c. c.* crus cerebri; *c. h*1. parencephalon; *c. h*2. temporal lobe; *c ma.* corpus mammillare; *f. m.* foramen of Monro; *inf.* infundibulum; *ly.* lyra; *m. o.* medulla oblongata; *o. ch.* optic chiasma; *olf.* olfactory lobe; *pty.* pituitary body; *vl. ip.* velum interpositum; *v. vn.* valve of Vieussens; *II*, optic nerve. (From Parker's *Zootomy*.)

hippocampal sulcus, on the inner surface of the temporal lobe. Internally the two hippocampi merge in a median area—the *lyra* (*ly.*).

Running along the anterior edge of the hippocampus is a ridge of fibres—the *tænia hippocampi* or *fimbria*—which passes down into the descending cornu. The union of the two tæniæ forms a median longitudinal strand, the *body of the fornix*, which, as already explained, lies below the corpus callosum, continuous with the splenium of the latter behind, but diverging from it anteriorly by dipping down towards the base of the brain. In the angular space between the corpus callosum above and the fornix below is the septum lucidum with the fifth ventricle. The tæniæ hippocampi are the *posterior pillars* of the fornix (*p. fo.*); the *anterior pillars* (*a. fo.*) are a pair of vertical bands which pass from the anterior end of the body downwards to the corpus mammillare at the base of the diencephalon.

Lying immediately in front of the hippocampus major is a vascular membrane, the *choroid plexus* (*ch. pl.*); this passes inwards to join its fellow of the opposite side through a transverse passage, the *foramen of Monro* (*f. m.*), which opens behind into the diacœle. The floor of the anterior cornu is formed of an eminence of gray matter—the *corpus striatum* (*cp. s.*). The right and left corpora striata are connected together by a narrow transverse band of white fibres—the *anterior commissure* (*a. co.*)—situated in front of the anterior pillars of the fornix.

The diacœle (v^3.) is a laterally compressed cavity, the roof of which is formed by a delicate vascular membrane, the *velum interpositum* (*vl. ip.*). On the upper surface of this is a network of blood-vessels continuous with the choroid plexuses of the lateral ventricle. From the posterior part of the roof of the diacœle arise the peduncles of the pineal body, and just behind their point of origin is the *posterior commissure* (*p. co.*), a delicate transverse band of fibres connecting together the posterior parts of the *optic thalami*. The latter (*o. th.*) are large masses of mixed gray and white matter forming the lateral portions of the diencephalon; they are connected together by a thick mass of gray matter, the *middle* or *soft commissure* (*m. co.*) passing across the diacœle. A rounded elevation near the anterior end of the external surface of each thalamus is the *corpus geniculatum* (*c. gn.*). Between the optic thalamus and the corpus striatum is a thin band of white matter—the *tænia semicircularis* (*t.s.*). The anterior boundary of the diacœle is a thin vertical lamina—the *lamina terminalis*—of which the septum lucidum is a mesial anterior prolongation. The floor of the diencephalon is produced downwards into a mesial rounded process, the *tuber cinereum* or *infundibulum* (*inf.*), to which the pituitary body is attached. In front of this, on the ventral aspect of the brain, is a thick curved transverse band of nerve fibres, the united *optic tracts*, from the anterior border of which the optic nerves are given off. Behind the tuber cinereum is a rounded elevation, the *corpus mammillare* (*c. ma.*).

In the mid-brain the dorsal part is remarkable for the fact that each *optic lobe* is divided into two by a transverse furrow, so that two pairs of lobes ($o.l.^1, o.l.^2$), the *corpora quadrigemina* are produced. On the ventral region of the mid-brain the *crura cerebri* are far more prominent than in the lower groups. In the hind-brain the *cerebellum* (Fig. 1031, *cb′. cb″.*) is very large; it consists of a *central lobe* or *vermis* and two *lateral lobes*, divided by very numerous fissures or sulci into a large number of small convolutions. Each lateral lobe bears an irregularly shaped prominence, the *flocculus*. On section (Fig. 1033, *cb.*) the cerebellum exhibits a tree-like pattern (*arbor vitæ*) brought about by the arrangement of the white and gray matter. On the ventral aspect of the hind-brain a flat band of transverse fibres—the *pons Varolii*—connects together the

lateral parts of the cerebellum. The cerebellum is connected with the other parts of the brain by three pairs of peduncles, the *anterior*, connecting it with the posterior optic lobes, the *middle*, passing on each side into the pons Varolii, the *posterior*, connecting it with the dorsal portion of the medulla oblongata. Between the anterior peduncles extends a transverse band, the *valve of Vieussens* (Fig. 1033, *v. vn.*), connected by its anterior edge with the corpora quadrigemina. Behind this is a short tract of transverse fibres—the *corpus trapezoideum*—and behind this again is a slightly elevated area marking the position of the *olivary body.* The floor of the fourth ventricle presents a median groove which ends posteriorly in a pointed depression—*calamus scriptorius*—leading into the central canal of the spinal cord.

The cranial nerves are similar to those of the Pigeon in most respects, differing in some of the particulars of their arrangement and distribution.

The Rabbit, like most other Vertebrates, possesses a *sympathetic nervous system*, consisting of a series of ganglia united together by commissural nerves, and giving off branches to the various internal organs. Two sympathetic ganglia are situated on each side in the neck—the *anterior* and *posterior cervical ganglia.* From the anterior nerve-branches pass forwards to enter the cranial cavity; from the posterior a nerve cord passes backwards to the first thoracic ganglion. Of the *thoracic ganglia* there are twelve on each side. From one of the more posterior of these originates the *splanchnic nerve* which passes backwards into the abdomen, ending in a ganglion—the *cœliac.* In the abdomen there are, on each side, twelve ganglia, the chain ending behind in a single *ganglion impar.*

In the **organs of special sense** the following special features are to be seen when a comparison is made with the Pigeon or Lizard. In the eye, the sclerotic is composed entirely of dense fibrous tissue; the pecten is absent. In the ear the principal point of difference is in the special development of the *cochlea.* This part of the membranous labyrinth, instead of retaining the simple curved form which it presents in the Bird, is coiled on itself in a close spiral of two-and-a-half turns. The spiral channel in the substance of the bone, in which this cochlear spiral runs, contains three passages; the middle one, much the smallest, being the *membranous cochlea*, the uppermost the *scala vestibuli*, and the lowermost the *scala tympani.*

The special features of the middle ear with its auditory ossicles have been already referred to.

Urinogenital Organs.—The kidneys are of somewhat compressed oval shape, with a notch or *hilus* on the inner side. They are in close contact with the dorsal wall of the abdominal cavity, the right being somewhat in advance of the left. Towards the

hilus the tubules of the kidney converge to open into a wide chamber—the *pelvis*—which forms the dilated commencement of the ureter. When the kidney is cut across, its substance is seen to be divided into a central mass or *medulla* and a peripheral portion or *cortex*. An *adrenal* (*suprarenal*) *body* lies in contact with the anterior end of each kidney. The *ureter* (Fig. 1034, *ur.*) runs backwards to open not into a cloaca, but directly into the *urinary bladder* (*bl.*). The latter is a pyriform sac with elastic walls which

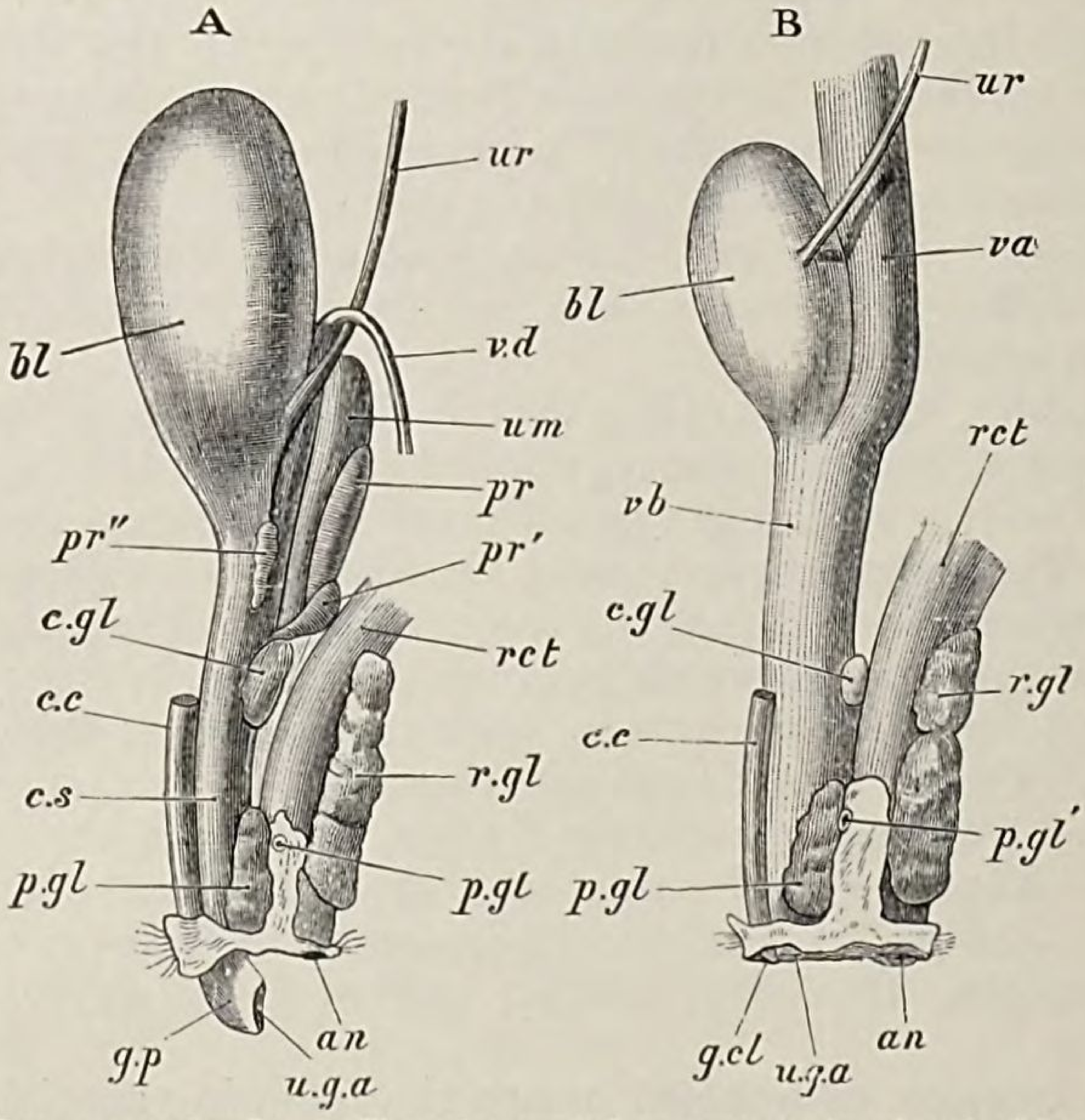


FIG. 1034.—**Lepus cuniculus.** The urino-genital organs; *A*, of male; *B*, of female, from the left side (half nat. size). The kidneys and proximal ends of the ureters, in *A* the testes, and in *B* the ovaries, Fallopian tubes and uteri are not shown. *an.* anus; *bl.* urinary bladder; *c. c.* corpus cavernosum; *c. s.* corpus spongiosum; *c. gl.* Cowper's gland; *g. cl.* glans clitoridis; *g. p.* glans penis; *p. gl.* perineal gland; *p. gl'.* aperture of its duct on the perineal space; *pr.* anterior, *pr'.* posterior, and *pr''.* lateral lobes of prostate; *rct.* rectum; *r. gl.* rectal gland; *u.g. a.* urinogenital aperture; *u. m.* uterus masculinus; *ur.* ureter; *va.* vagina; *vb.* vestibule; *v. d.* vas deferens. (From Parker's *Zootomy.*)

vary in thickness according as the organ is dilated or contracted. In the male the openings of the ureters are situated much nearer the posterior narrower end or neck than in the female.

In the male Rabbit the *testes* are oval bodies, which, though in the young animal they occupy a similar position to that which they retain throughout life in the Pigeon, pass backwards and downwards as the animal approaches maturity, until they come to lie each in a *scrotal sac* situated at the side of the urinogenital opening. The cavity of each scrotal sac is in free communication with the cavity of the abdomen by an opening—the *inguinal canal*. The sperms have an oval compressed head 0·005 mm. in length and a slender "tail" 0·045 mm. long. A convoluted *epididymis*

closely adherent to the testis, forms the proximal part of the *vas deferens.* The *vasa deferentia* (*v. d.*) terminate by opening into a urinogenital canal, or *urethra,* into which the neck of the urinary bladder is continued. A *prostate gland* (*pr.*) surrounds the commencement of the urethra, the neck of the bladder and the terminal parts of the vas deferentia. A diverticulum of the urethra —the *uterus masculinus* (*u. m.*)—lies embedded in the prostate gland close to the neck of the bladder. A small pair of ovoid glands, *Cowper's glands* (*c. gl.*), lie just behind the prostate close to the side of the urethra.

The terminal part of the urethra traverses a cord of vascular tissue, the *corpus spongiosum* (*c. s.*), which forms the dorsal portion of the penis. The greater part of the penis is formed of two closely approximated firm cords of vascular tissue—the *corpora cavernosa* (*c. c.*) which are attached proximally to the ischia; and it terminates in the slightly dilated, soft, conical *glans penis* (*g. p.*). A loose fold of skin, the *prepuce,* encloses the penis. A pair of glands with an odorous secretion, the *perineal glands* (*p. gl.*), open at the sides of the penis: two similar glands, the *rectal glands* (*r. gl.*), lie at the sides of the rectum.

In the female the *ovaries* (Fig. 1035, *ov.*) are small ovoid bodies attached to the dorsal wall of the abdomen behind the kidneys. The *Graafian follicles* enclosing the ova form only very small rounded projections on their outer surface.

The *oviducts* in the anterior part of their extent (*Fallopian tubes, fl.t.*) are very narrow and slightly convoluted. They open into the abdominal cavity by wide funnel-shaped openings, (*fl.t'.*) with fimbriated or fringed margins. Posteriorly each passes into a thick-walled *uterus* (*r. ut.*). The two uteri open separately into a median tube, the *vagina* (*va.*). The *vestibule* (Fig. 1034, *vb.*), or urinogenital canal, is a wide median passage, into which the vagina and the bladder open.

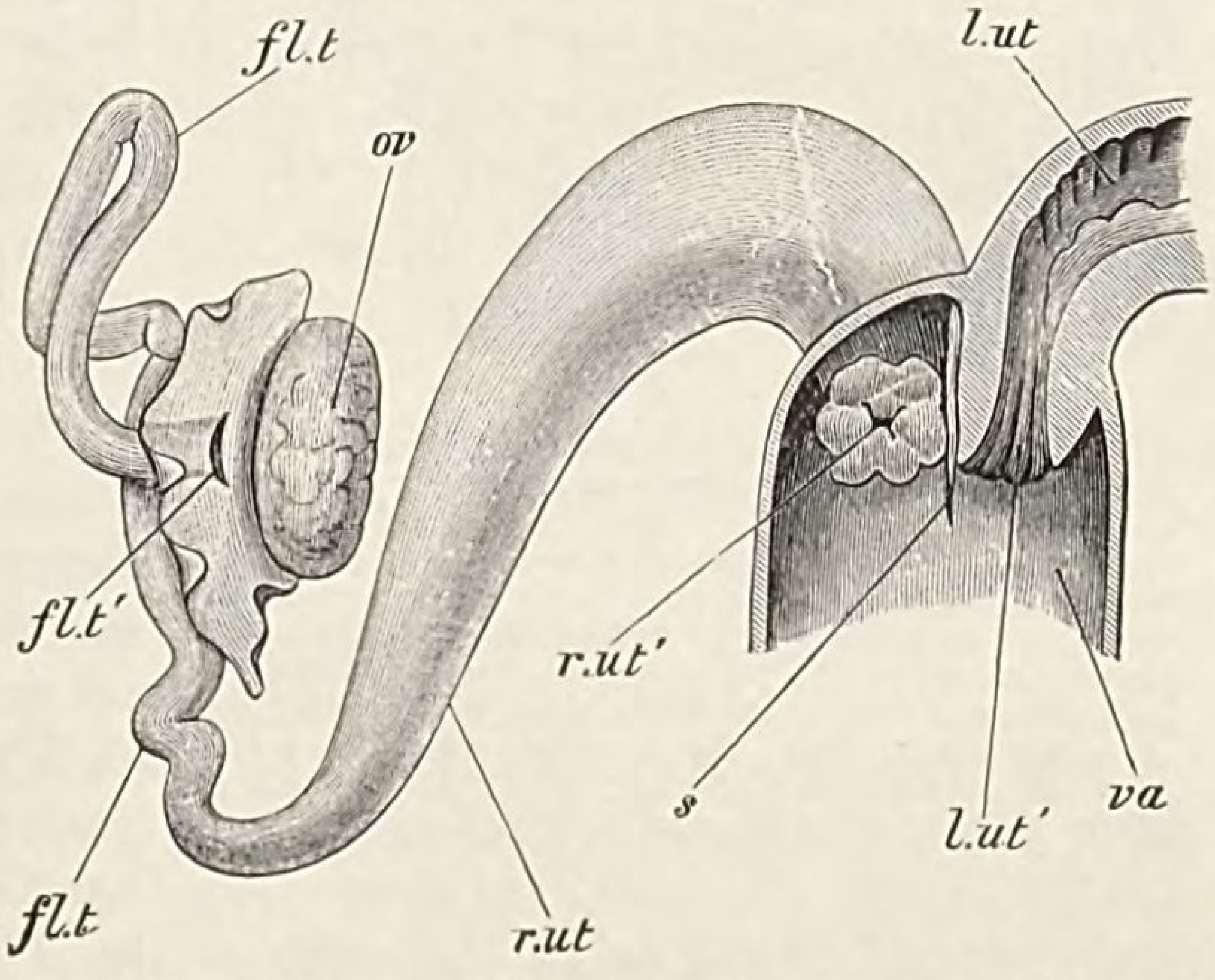


FIG. 1035.—**Lepus cuniculus.** The anterior end of the vagina, with the right uterus, Fallopian tube and ovary (nat. size). Part of the ventral wall of the vagina is removed, and the proximal end of the left uterus is shown in longitudinal section; *fl. t.* Fallopian tube; *fl. t'.* its peritoneal aperture; *l. ut.* left uterus; *l. ut'.* left os uteri; *r. ut.* right uterus; *r. ut'.* right os uteri; *s.* vaginal septum; *va.* vagina. (From Parker's *Zootomy.*)

On its ventral wall is a small, hard, rod-like body, the *clitoris* (*c. c.*), corresponding to the penis of the male, and composed of two very short *corpora cavernosa* attached anteriorly to the ischia, with a terminal soft conical *glans clitoridis* (*g. cl.*). The *vulva*, or external opening of the vestibule, is bounded laterally by two prominent folds—the *labia majora*.

Development.—The Rabbit is viviparous. The ovum, which is of relatively small size, after it has escaped from its Graafian follicle, passes into the oviduct, where it becomes fertilised, and reaches the uterus, in which it develops into the *fœtus*, as the intra-uterine embryo is termed. The young animal escapes from the uterus in a condition in which all the parts have become fully formed, except that the eyelids are still closed, and the hairy covering is not yet completed. As many as eight or ten young are produced at a birth, and the period of gestation, *i.e.*, the time elapsing between the fertilisation of the ovum and the birth of the young animal, is thirty days. Fresh broods may be born once a month throughout a considerable part of the year, and, as the young Rabbit may begin breeding at the age of three months, the rate of increase is very rapid.

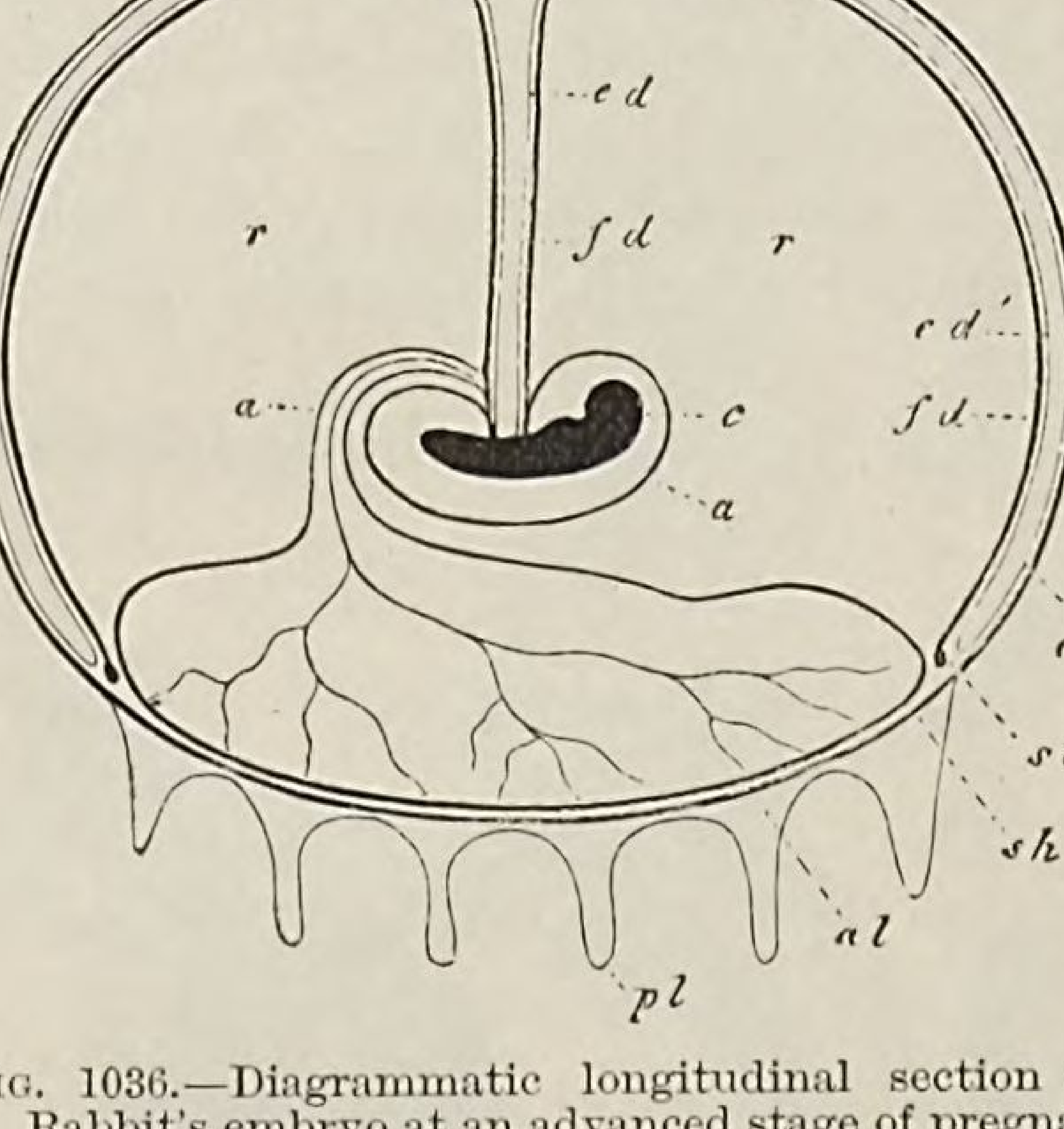


FIG. 1036.—Diagrammatic longitudinal section of a Rabbit's embryo at an advanced stage of pregnancy. *a.* amnion; *a*, urachus; *al.* allantois with blood-vessels, *ds*, cavity of yolk-sac; *c.* embryo; *ed.* endodermal layer of yolk-sac; *ed'.* inner portion of endoderm; *ed''.* outer portion of endoderm lining the compressed cavity of the yolk-sac; *fd.* vascular layer of yolk-sac; *pl.* placental villi; *r.* space filled with fluid between the amnion, the allantois and the yolk-sac; *sh*, subzonal membrane; *st.* sinus terminalis. (From Balfour, after Bischoff.)

The segmentation is of the holoblastic type. An amnion and an allantois are developed much as in the case of the Bird (p. 412). But the later history of these fœtal membranes is widely different in the Rabbit, owing to the modifications which they undergo, in order to take part in the formation of the *placenta*—the structure by whose instrumentality the fœtus receives its nourishment from the walls of the uterus. The placenta is formed from the serous membrane, or outer layer of the amniotic fold, in a limited disc-shaped area, in which the distal portion of the allantois coalesces with it. The membrane thus formed (*chorion*) develops vascular processes—the *chorionic villi*—which are received into depressions (the *uterine crypts*) in the mucous membrane of the uterus. The

completed placenta with its villi is supplied with blood by the allantoic vessels. The placenta of the Rabbit is of the type termed *deciduate*, the villi of the placenta being intimately united with the uterine mucous membrane, and a part of the latter coming away with it at birth in the form of a *decidua*, or after-birth.

2. Distinctive Characters and Classification

The Mammalia are air-breathing Vertebrates, with warm blood, and with an epidermal covering in the form of hairs. The bodies of the vertebræ are in nearly all Mammals ossified each from three independent centres, one of which develops into the centrum proper, while the others give rise to thin discs of bone—the epiphyses. Also characteristic of the spinal column of Mammals are the discs of fibro-cartilage termed inter-vertebral discs, which intervene between successive centra.

The skull has two condyles for connection with the atlas, instead of the single condyle of the Sauropsida ; and the lower jaw articulates with the skull in the squamosal region without the intermediation of the separate quadrate element always present in that position in Birds and Reptiles.

Each of the long bones of the limbs is composed in the young condition of a central part or shaft and terminal epiphyses, the latter only becoming completely united with the shaft at an advanced stage.

In the pectoral arch the coracoid of the Birds and Reptiles is usually represented only by a vestige or vestiges, which unite with the scapula in the adult.

Mammals are typically *diphyodont, i.e.*, have two sets of teeth —a milk or deciduous set, and a permanent set: some are *monophyodont, i.e.*, have only one set. The teeth are *thecodont, i.e.*, the base of each tooth is embedded in a distinct socket or alveolus in the substance of the bone of the jaw; and nearly always the teeth in different parts of the jaw are clearly distinguishable by differences of shape into incisors, canines, and grinding teeth, *i.e.*, are *heterodont;* in some instances the teeth are all alike (*homodont*). A cloaca is absent except in the Prototheria.

A movable plate of cartilage—the epiglottis—represented only by a rudiment in some Amphibia and Sauropsida—overhangs the slit—commonly termed glottis—leading from the pharynx into the cavity of the larynx.

A partition of muscular fibres usually with a tendinous centre—the diaphragm—divides the cavity of the body into two parts, an anterior—the thorax—containing the heart and lungs, and a posterior—the abdomen—containing the greater part of the alimentary canal with its associated glands—the liver and pancreas —and the renal and reproductive organs.

The lungs are freely suspended within the cavity of the thorax.

The heart is completely divided into two halves—a right and a left—between which there is no aperture of communication. Each half consists of an auricle and a ventricle, opening into one another by a wide opening, guarded by a valve composed of three membranous cusps on the right side, two on the left. The right ventricle gives off the pulmonary artery; the left gives off the single aortic arch, which passes over to the left side, turning round the left bronchus in order to run backwards as the dorsal aorta: it therefore represents the left aortic arch of Reptiles. The blood is warm. The red blood corpuscles are non-nucleated and usually circular.

The two cerebral hemispheres, in all but the Monotremes and Marsupials, are connected together by a band of transverse fibres —the corpus callosum—not represented in the lower Vertebrates. The dorsal part of the mid-brain is divided into four optic lobes—the corpora quadrigemina. On the ventral side of the hind-brain is a transverse band of fibres—the pons Varolii—by which the lateral portions of the cerebellum are connected together.

The ureters, except in the Prototheria, open into the bladder.

Mammals are all, with the exception of the Monotremes, viviparous. The fœtus is nourished before birth from the blood-system of the parent through a special development of the fœtal membranes and the lining membrane of the uterus, termed the placenta. After birth the young Mammal is nourished for a longer or shorter time by the milk, or secretion of the mammary glands of the parent.

Sub-class I.—Prototheria.

Mammals in which the mammary glands are devoid of teats; the oviducts are distinct throughout, and there is a cloaca into which the ureters and urinary bladder open separately. In the centra of the vertebræ the epiphyses are absent or imperfectly developed; the bones of the skull early coalesce by the obliteration of the sutures; there is a large coracoid articulating with the sternum, and a ⊤-shaped episternum, and there is a pair of epipubic (marsupial) bones. A corpus callosum is absent. The ova are meroblastic, and are discharged in an early stage of their development, enclosed in a tough shell.

This sub-class comprises a single living order, the *Monotremata*, including the Duck-Bill or Platypus (*Ornithorhynchus*) and the Spiny Anteater (*Echidna*), together probably with an imperfectly known extinct, Secondary and early Tertiary order, the *Multituberculata*.

Sub-class II.—Theria.

Mammals in which the mammary glands are provided with teats; the oviducts are united in a longer or shorter part of their extent, and there is no cloaca; the ureters open into the base

of the bladder. The centra of the vertebræ possess distinct epiphyses; the bones of the skull in most instances do not completely coalesce, most of the sutures remaining distinguishable throughout life; the coracoid is represented by vestiges, and an episternum is absent as a distinct bone. The ova are (except in some Marsupials) holoblastic, and the early development of the young takes place in the uterus.

SECTION A.—METATHERIA (MARSUPIALIA).

Theria in which the young, born in a comparatively rudimentary condition, are sheltered during their later development in an integumentary pouch—the *marsupium*. A common sphincter muscle surrounds anus and urinogenital aperture. The tympanic cavity is partly bounded by the alisphenoid; the jugal furnishes a part of the glenoid cavity for the condyle of the mandible; there are well-developed epipubic bones. There is no corpus callosum. When a placenta is present, it is functional only for a short period.

ORDER 1.—POLYPROTODONTIA.

Marsupials with numerous, small, sub-equal incisor teeth, and large canines; the molars provided with sharp cusps.

This order includes the Opossums (*Didelphyidæ*), the Dasyures (*Dasyuridæ*), the Bandicoots (*Peramelidæ*).

ORDER 2.—DIPROTODONTIA.

Marsupials with not more than three incisors on each side in the upper jaw, and usually only one in the lower; the central incisors large, the canines usually small or absent; the molars blunt, with tubercles or transverse ridges.

This order includes the Wombats (*Phascolomyidæ*), the Phalangers (*Phalangeridæ*), and the Kangaroos (*Macropodidæ*).

SECTION B.—EUTHERIA.

Theria in which a marsupium is absent, and the young are always nourished *in utero*, for a relatively considerable period, through the agency of a placenta. The anus and urinogenital aperture are not surrounded by a common sphincter. The alisphenoid never contributes to the formation of the wall of the tympanic cavity; except in the thyrocoidea and some Rodents, the jugal takes no part in bounding the glenoid cavity, and there are no marsupial bones. A corpus callosum is present.

ORDER 1.—EDENTATA.

Eutheria, in which the teeth are absent in the adult or the dentition is imperfect, incisors and canines being seldom repre-

sented, and, though there may be numerous pre-molars and molars, these never form roots and are devoid of enamel. All, with the exception of two genera, are monophyodont. The sacral vertebræ are frequently in excess of the number usual in other orders. The coracoid process is usually relatively larger than in other Eutheria, and does not become completely fused with the scapula. The brain is sometimes of low, sometimes of comparatively high organisation.

There are five families comprised in the order, each characterised by the presence of a number of remarkable peculiar features, viz., the Sloths (*Bradypodidæ*) the American Anteaters (*Myrmecophagidæ*) the Armadillos (*Dasypodidæ*) the Scaly Anteaters (*Manidæ*) and the Cape Anteaters (*Orycteropodidæ*).

Order 2. Cetacea.

Aquatic Eutheria with large head, fish-like fusiform body, devoid of hairy covering, with the pectoral limbs paddle-like, the pelvic limbs absent, and with a horizontal caudal fin. A vertical dorsal fin is usually present. There is a long snout and the nostrils open by two lateral external apertures or a single median one situated in all the recent forms far back towards the summit of the head. The cervical region of the spinal column is very short, and its vertebræ usually completely united together. Clavicles are absent. The humerus is freely movable at the shoulder, but all the other articulations of the limb are imperfect. The phalanges of the second and third digits always exceed in number the number (three) normal in the Mammalia. The pelvis is represented by a pair of horizontally placed styliform vestiges of the ischia. Teeth may be absent and their place taken by sheets of *baleen* or "whalebone"; when present they may be very numerous and homodont, or less numerous and heterodont, or reduced to a single pair. The epiglottis and arytenoids are prolonged, and embraced by the soft palate, so as to form a continuous tube for the passage of the air from the nasal cavities to the trachea. The brain is large, and the cerebral hemispheres are richly convoluted. The testes are abdominal. The teats are two, and are posterior in position. The uterus is two-horned, the placenta diffuse and non-deciduate (*vide infra*).

This order includes the Baleen Whales (*Balænidæ*), Sperm Whales (*Physeter*), Killers (*Orca*), Porpoises (*Phocæna*), and Dolphins (*Delphinus*).

Sub-order a.—Archæoceti (Zeuglodonta).

Extinct Cetacea in which the premaxillæ take a considerable share in the formation of the elongated rostrum, and in which the nasals are long and narrow and the nostrils comparatively far

forwards. The teeth are heterodont, the anterior teeth being simple and pointed, the posterior compressed, with two fangs and denticulated cutting edges.

This sub-order comprises only one known genus—*Zeuglodon*—of Tertiary age.

Sub-order b.—Mystacoceti.

Cetacea in which plates of baleen are developed. Functional teeth are never present, and the premaxillæ are narrow and take only a small share in the formation of the rostrum. The nostrils are situated far back. The nasal cavities are roofed over by the nasals. The tympanic bones are scroll-like and are fused with the periotics. The rami of the mandible are not united anteriorly.

This sub-order includes the Whale-bone Whales (*Balæna* and others).

Sub-order c.—Odontoceti.

Cetacea in which the premaxillæ are narrow and the nostrils far back as in the Mystacoceti. The nasals are reduced and do not roof over the nasal cavities. The tympanic bones are not scroll-like, and do not become fused with the periotic. The rami of the mandible are united at the symphysis. Baleen plates are never present, and teeth are developed and are usually very numerous and homodont. This sub-order comprises the Porpoises (*Phocæna*), Dolphins (*Delphinus* and others), and *Killers* (*Orca*), the Sperm-whales (*Physeter* and *Cogia*), the Bottle-nosed Whales (*Hyperoödon*) and Beaked Whales (*Mesoplodon*), and the extinct Squalodonts.

Order 3.—Sirenia.

Aquatic Eutheria with moderate-sized head and fish-like, depressed fusiform body, with the pectoral limbs paddle-like, the pelvic absent, and with a horizontally expanded tail fin. There is no vertical dorsal fin. There is a very thick wrinkled integument devoid of or with only a scattered covering of hairs. The snout is not greatly elongated, and the nostrils open by a pair of valvular apertures on its upper surface. The cervical vertebræ (of which there are only six in the Manatee) are not fused. A clavicle is absent. There is a distinct, though small, articulation between the humerus and the bones of the forearm. There are never more than three phalanges in any of the digits. The pelvis is represented by a pair of vertically situated vestiges. The anterior part of the palate and the symphysis of the mandible (which is prolonged) are covered with rugose horny plates. The epiglottis and arytenoids are not prolonged as they are in the Cetacea. The brain is comparatively small, and the convolutions are not highly developed. The testes are abdominal. The teats are two and pectoral in

position. The uterus is two-horned. The placenta is non-deciduate and zonary.

This order includes only the Dugong (*Halicore*), the Manatee (*Manatus*) and the recently extinct *Rhytina*.

ORDER 4.—UNGULATA.

Terrestrial, chiefly herbivorous, Eutheria, with the fur abundant or scanty, with the terminal phalanges, on which the weight of the body usually rests, nearly always invested in solid horny hoofs. The teeth are heterodont and diphyodont; the canines usually absent or small, and the pre-molars and molars well-developed, with broad crowns having tuberculated or ridged surfaces. The clavicle is absent; the humerus has no foramen over the inner condyle: the scaphoid and lunar of the carpus are always distinct. The villi of the placenta are diffuse or gathered into patches—the *cotyledons*.

SECTION 1.—UNGULATA VERA.

Ungulata in which the feet are always digitigrade, with never more than four functional digits. The os magnum of the carpus articulates with the scaphoid. The testes are contained in a scrotum. The teats are usually four, and situated far back, never exclusively thoracic in position. The uterus is two-horned, The allantois is large; the placenta is non-deciduate, and the villi diffuse or gathered into cotyledons.

This section comprises all the typical Ungulates.

Sub-order a.—Perissodactyla.

Ungulata vera in which the third toe of both manus and pes is larger than the others and symmetrical in itself, and in which there is a tendency to reduction of the others. The femur has a third trochanter. The tibial articular surface of the astragalus is pulley-shaped; the distal surface flat and more extensively related with the navicular than with the cuboid; the calcaneum does not articulate with the fibula. The pre-molars and molars are complexly folded, and the posterior pre-molars usually resemble the molars in size and pattern. The stomach is simple; the cœcum large. There is never a gall-bladder. The teats are situated in the groin, and the placenta is diffuse.

This sub-order includes the Horses, Asses, and Zebras (*Equidæ*), the Tapirs (*Tapirus*), and the Rhinoceroses (*Rhinoceros*).

Sub-order b.—Artiodactyla.

Ungulata vera in which the third and fourth digits of both manus and pes form a symmetrical pair, and in which the others

are usually absent or vestigial. The femur has no third trochanter. The tibial surface of the astragalus is flat, the distal surface articulates largely with the cuboid, and the calcaneum has a flat articular surface for the fibula. The pre-molars are smaller than the molars. The stomach is almost always complex, and the cœcum is small. The teats are few and situated in the groin, or numerous and extending along the abdomen. The placenta is diffuse or cotyledonary.

This sub-order includes the *Ruminants*, such as the Camels (*Camelidæ*), Oxen (*Bovidæ*), Sheep (*Ovis*), Goats (*Capra*), Antelopes, Giraffes (*Giraffa*), and Deer (*Cervidæ*), and the *Non-Ruminants*, viz., the Pigs (*Sus*), Peccaries (*Dicotyles*), and Hippopotami (*Hippopotamus*).

Sub-order c.—Litopterna.

Extinct Ungulates with the digits of the manus and pes (which are never more than three in each) elongate, and of the Perissodactyle type. The astragalus has a pulley-shaped articular surface for the tibia as in the Perissodactyla, while the calcaneum has a small facet for the fibula as in the Artiodactyla. The bones of the carpus and tarsus do not interlock as in existing Ungulata vera, but are arranged in vertical series. A third trochanter is present, but is smaller than in the Perissodactyla.

This sub-order includes *Macrauchenia* and other genera, the remains of which have only been found in the Tertiary deposits of Patagonia and Bolivia.

Sub-order d.—Astrapotheria.

Extinct Ungulates with the digits of the manus and pes, of which there were probably five in each, comparatively short. The astragalus has a flat articular surface for the tibia. The carpal and tarsal bones do not interlock. Sometimes there is a pair of large tusks in each jaw. The molar teeth have a more or less marked resemblance to those of the Rhinoceroses.

This sub-order includes only two genera—*Astrapotherium* and *Homalodontotherium*—both confined to the Tertiary deposits of Patagonia.

SECTION 2.—SUBUNGULATA.

Ungulata in which the feet may be plantigrade and there may be five functional digits. The magnum of the carpus does not articulate with the scaphoid, at least in living forms.

Sub-order a.—Hyracoidea.

Small Subungulata with furry integument, with four completely formed digits in the fore-foot (the pollex being vestigial), and

three in the hind-foot (the hallux being absent and the fifth digit vestigial). The ungual phalanges of the four complete digits of the fore-foot are small, somewhat conical and flattened; that of the second digit of the hind-foot is deeply cleft, and has a long curved claw; the rest of the digits of the hind-foot have broad nails. There are no canines, and in the upper jaw there is only a single pair of incisors, which resemble those of the Rodents in their elongated curved form and in growing from persistent pulps. The thoracic and lumbar vertebræ are very numerous (28–30), twenty-one or twenty-two bearing ribs. The tail is very short. Clavicles are absent. There is a centrale in the carpus. The stomach is divided into two parts by a constriction. The large intestine has connected with it a pair of large supplementary cœca. There is no gall-bladder. The testes do not descend into a scrotum. There are six teats, four in the groin and two in the axillæ. The villi surround the placenta in a broad band (zonary placenta).

This sub-order includes only a single family, the *Hyracidæ*, with two genera, *Hyrax* and *Dendrohyrax*.

Sub-order b.—Proboscidea.

Large Subungulata with greatly thickened integument scantily furnished with hair, with massive limbs, each having five complete digits united by skin, but each terminating in a distinct hoof; and with the nose produced into a long flexible and prehensile proboscis or trunk, at the end of which the external nares are situated. In existing forms only a single pair of incisors is present, situated in the upper jaw, and developed into enormous tusks. There are no canines, and the molars are large and transversely ridged. The stomach is simple. The testes do not descend into a scrotum. There are two teats, situated on the thorax. The uterus is two-horned, the placenta non-deciduate and zonary.

This sub-order includes only the Elephants (*Elephas*), the Mammoths, Mastodons, and other extinct forms.

Sub-order c.—Pyrotheria.

A group of South American Tertiary hoofed Mammals comprising a single genus—*Pyrotherium*—of doubtful affinities, perhaps allied to the Proboscidea. The teeth resemble those of the extinct Proboscidean *Dinotherium*.

Sub-order d.—Amblypoda.

Extinct Subungulata with plantigrade limbs, each provided with five short digits having broad terminal phalanges. A third trochanter is sometimes present, sometimes absent. Carpal and tarsal bones interlock to some extent, and the fibula articulates

with the calcaneum. The brain-case is very small. Upper incisors are sometimes wanting. Both upper and lower canines are present, and the former are sometimes produced into elongated tusks. The pre-molars and molars are of a simple and primitive pattern. In some (*Uintatherium* and allies) the skull bears three pairs of processes which may have been of the nature of horn-cores.

The Amblypoda comprise *Coryphodon*, *Uintatherium*, and other Tertiary forms, both European and American.

Sub-order e.—Toxodonta.

Extinct Ungulates with massive skull, short, stout limbs, each with three sub-equal digits. While the carpal bones interlock, the tarsals are arranged in vertical series. The tibial articular surface of the astragalus is nearly flat. The pre-molar and molar teeth in *Toxodon* all grow from persistent pulps, in the other genera they are rooted.

This sub-order comprises *Toxodon* and other genera from the South American Tertiary beds.

Sub-order f.—Condylarthra.

Extinct (Eocene) Subungulata with usually five digits with pointed terminal phalanges, in manus and pes, with an entepicondylar foramen and a third trochanter. The carpal and tarsal bones do not interlock so completely as in the Ungulata vera. The dentition is complete, and the teeth frequently exhibit resemblances to those of the Carnivora.

This sub-order comprises *Phenacodus*, *Periptychus*, and other Eocene forms.

A group of extinct Manuals, the *Tillodontia*, the affinities of which are uncertain, may be mentioned here. They appear to combine in a remarkable manner Ungulate with Carnivorous and Rodent features.

ORDER 5.—CARNIVORA.

Mostly carnivorous Eutheria with furry integument, with never less than four well-developed digits in each manus and pes, all provided with claws which are frequently more or less retractile. The pollex and hallux are never capable of being opposed to the other digits. The clavicle is frequently absent, and, when present is never complete. There is often a foramen over the inner condyle of the humerus. The scaphoid and lunar of the carpus are always united, and there is never an os centrale.

They are diphyodont and heterodont, and the teeth are provided with roots. The incisors, usually three pairs in the upper and three in the lower jaw, are small and chisel-shaped. The canines are

usually large, conical, curved, and pointed. The pre-molars and molars are usually compressed and trenchant, especially the most anterior. The stomach is simple; the cœcum, when present, is small. The brain is usually highly developed, and the cerebral hemispheres always convoluted. The teats are abdominal. The uterus is two-horned; the placenta deciduate and nearly always zonary.

Sub-order a.—Carnivora vera.

Carnivora which have the limbs nearly always adapted for a terrestrial existence, with all the digits usually provided with claws which may be retractile into a sheath. The first digit of the manus and the first and fifth of the pes are never longer than the others. One tooth on each side in each jaw, the last pre-molar in the upper jaw and the first molar in the lower, is always modified to form the carnassial or sectorial tooth, with a cutting edge which bites against the edge of the opposed tooth.

This sub-order comprises the Cats (*Felidæ*), Civets (*Viverridæ*), Hyænas (*Hyænidæ*), Dogs (*Canidæ*), Bears (*Ursidæ*), Weasels (*Mustelidæ*) and Otters (*Lutridæ*).

Sub-order b.—Pinnipedia.

Carnivora in which the limbs are adapted to an aquatic life, the proximal segments being short, the distal elongated and webbed between the digits, with five well-developed digits in each manus and pes, the first and fifth of the pes being larger than the others. The number of incisors is reduced, and there are no carnassials. The cerebral hemispheres are very richly convoluted.

This order includes the Eared Seals (*Otariidæ*), the Earless Seals (*Phocidæ*) and Walruses (*Trichechidæ*).

Sub-order c.—Creodonta.

Extinct Carnivora with plantigrade limbs and without carnassial teeth, with small brain cavities, and with the scaphoid and lunar usually separate.

The members of this group (which is confined to the Tertiary period) have some striking points of resemblance to the Insectivora, the Polyprotodont Marsupials and the extinct Condylarthra.

Order 6.—Rodentia.

Vegetable-feeding Eutheria, mostly of small size, with furry (sometimes spiny) integument, clawed digits, and usually plantigrade limbs. A clavicle is usually present. The dentition is diphyodont; there are no canines, and there are never more than two incisors in the lower jaw and usually only two in the upper,

all elongated, chisel-like, and growing from persistent pulps; the pre-molars and molars are usually few, and often also grow from persistent pulps. There is a large cœcum. The cerebral hemispheres have smooth surfaces, and do not much overlap the other parts of the brain. The testes are retained in the abdomen or descend to the groin. The uterus is two-horned or double. The placenta is deciduate and disc-shaped (discoidal).

This extensive order includes the Rats and Mice (*Muridæ*), Hares and Rabbits (*Leporidæ*), Squirrels (*Sciuridæ*), Jerboas (*Dipodidæ*), Beavers (*Castoridæ*) and Porcupines (*Hystricidæ*.)

ORDER 7.—INSECTIVORA.

Small insectivorous Eutheria with the nose usually produced into a short soft muzzle, with furry (sometimes spiny) integument, clawed digits, and usually pentadactyle plantigrade limbs. The dentition is diphyodont and complete, and all the teeth are rooted; the incisors are small; there are never fewer than two incisors on each side of the lower jaw; the molars are small and provided with pointed cusps. A clavicle is present. The brain is simple and devoid of convolutions. The testes are situated in the groin, and are not enclosed in a scrotum. The uterus is two-horned or double. The placenta is deciduate and discoidal.

Included in this order are the Moles (*Talpidæ*), Shrews (*Soricidæ*), and Hedgehogs (*Erinaceidæ*).

ORDER 8.—CHIROPTERA.

Eutheria in which the pectoral limbs are modified to form wings, the bones, more especially those of the second to the fifth digits, being greatly elongated so as to support a broad web of skin extending back to the hind-limbs. The sternum has a keel for the attachment of the pectoral muscles, which play an important part in bringing about the movements of flight. The ulna is vestigial; the pollex is small, the remaining digits greatly elongated. The hind-limb is rotated outwards so that the knee is directed backwards. There is a cartilaginous rod (*calcar*) attached to the inner side of the ankle-joint and helping to support a fold of skin (interfemoral membrane) which extends from the hind-limbs to the tail or caudal region of the body. The cerebral hemispheres are smooth and do not overlap the cerebellum. The dentition is complete, heterodont and diphyodont. The penis is pendent; the testes abdominal or situated in the groin. The uterus is simple or bicornuate; the placenta deciduous and discoidal.

Sub-order a.—Megachiroptera.

Large frugivorous Chiroptera with elongated snout, without foliaceous appendages to the nose and ears, the second digit of the

manus terminating in a claw. The tail, when present, is not enclosed in the interfemoral membrane, but lies below it. The crowns of the molar teeth are devoid of sharp cusps.

This sub-order comprises the so-called Flying Foxes (*Pteropus*) of tropical and sub-tropical parts of the Eastern Hemisphere.

Sub-order b.—Microchiroptera.

Small, mostly insectivorous, Chiroptera, with short snout, frequently with foliaceous appendages of the nose and ears, the second digit of the manus never provided with a claw. The tail when present is enclosed in the inter-femoral membrane. The crowns of the molar teeth are provided with sharp cusps.

This sub-order includes all the ordinary Bats (*Vespertilio* and other genera).

ORDER 8.—PRIMATES.

Eutheria nearly all adapted to an arboreal life, the limbs being prehensile owing to the pollex and hallux being more or less completely opposable to the other digits. There are nearly always five digits, provided with flat nails in both manus and pes. The orbit is surrounded by a complete bony rim. The clavicles are in all cases well developed. There is no foramen above the inner condyle of the humerus, and the femur never has a third trochanter. The stomach is generally simple. The testes descend into a scrotum. There are nearly always two teats on the thoracic region. The placenta may be non-deciduate, or deciduate and meta-discoidal.

Sub-order a.—Prosimii.

Ape-like, mostly nocturnal, arboreal Primates of comparatively low organisation. All the digits of both feet are provided with flat nails, except the second of the hind-foot, which has a claw. Both the pollex and hallux are always well developed. The posterior bony rim of the orbit is a narrow bar beneath which there is a free communication between the orbit and the temporal fossa. The lacrymal foramen is situated outside the margin of the orbit. In nearly all cases the inner pairs of incisors of the upper jaw are separated by a median space. The cerebral hemispheres are not very highly developed, and do not completely overlap the cerebellum. There may be a pair of teats on the abdomen. The uterus is two-horned and the placenta diffuse.

This sub-order comprises the Lemurs (*Lemur*, *Tarsius* and other genera) and Aye-Ayes (*Chiromys*).

Sub-order b.—Anthropoidea.

Most highly organised Primates, chiefly modified for an arboreal life. The digits are all provided with flat nails, except in the

Hapalidæ, in which all except the hallux are provided with a claw. The pollex is in some rudimentary or absent. The orbit is separated from the temporal fossa by a broad vertical plate, and the lacrymal foramen is situated within the margin of the orbit. The inner upper incisors are in close contact. The cerebral hemispheres are usually richly convoluted, and completely, or nearly completely, cover over the cerebellum. The uterus has no horns. The placenta is deciduate and metadiscoidal.

Family i.—*Hapalidæ.*

Anthropoidea with the pollex not opposable, all the digits except the hallux provided with curved pointed claws, without cheek-pouches or ischial callosities, with a broad nasal septum, without bony external auditory meatus, and with a non-prehensile tail. The dental formula (*vide infra*) is $i. \frac{2}{2}, c. \frac{1}{1}, p. \frac{3}{3}, m. \frac{2}{2} = 32$.

This family includes the Marmosets (*Hapale*).

Family ii.—*Cebidæ.*

Anthropoidea with the pollex not opposable, all the digits provided with flat nails, without cheek-pouches or ischial callosities, with a broad nasal septum, and without bony external auditory meatus. The tail is sometimes prehensile. The dental formula is $i. \frac{2}{2}, c. \frac{1}{1}, p. \frac{3}{3}, m. \frac{3}{3} = 36$.

This family includes the Howling Monkeys (*Mycetes*), Tee Tees (*Callithrix*), Squirrel Monkeys (*Chrysothrix*), Spider Monkeys (*Ateles*), and Capuchin Monkeys (*Cebus*).

Family iii.—*Cercopithecidæ.*

Anthropoidea with the pollex, when present, opposable, with or without cheek-pouches, with ischial callosities, with a narrow nasal septum and a bony external auditory meatus. The tail is not prehensile. The sternum is narrow. The dental formula is $i. \frac{2}{2}, c. \frac{1}{1}, p. \frac{2}{2}, m. \frac{3}{3} = 32$. The cœcum is devoid of vermiform appendage.

This family includes the Baboons (*Cynocephalus*) and Macaques (*Macacus*).

Family iv.—*Simiidæ.*

Anthropoidea with the pollex opposable, without cheek-pouches, usually without ischial callosities, with a narrow nasal septum and a bony external auditory meatus. The pectoral limbs are much longer than the pelvic. The cœcum has a vermiform appendage

The centrale of the carpus is sometimes absent. The dental formula is the same as that of the preceding family.

This family includes the Gibbons (*Hylobates*), Orangs (*Simia*), Chimpanzees (*Anthropopithecus*), and Gorillas (*Gorilla*).

Family v.—*Hominidæ.*

Anthropoidea which differ from the Simiidæ mainly in the more perfect assumption of the erect posture, co-ordinated with alteration of the curvature of the spine, and with the more complete adaptation of the hind-limbs to bearing the weight of the body, in the absence of the power of opposition in the hallux, and its more complete development in the pollex, in the greater length of the hind- as compared with the fore-limbs, in the smaller size of the canine teeth, and the much greater size and complexity of the brain.

This family includes only the Human Species (*Homo sapiens*).

Systematic Position of the Example.

The genus Lepus, to which the common Rabbit belongs, comprises a number of other species, the common Hare being among the number, distinguished from one another by slight differences in the proportions of the parts and other general features. Lepus is the only genus of the family *Leporidæ*, which is associated with the family *Lagomyidæ* or Picas under the designation *Duplicidentata* owing to the presence in these two families, and in these two alone, of the entire order Rodentia to which they belong, of a second pair of incisors in the upper jaw. The chief distinctive features of the family Leporidæ are the elongated hind-limbs, the short recurved tail, the long ears, and the incomplete clavicles.

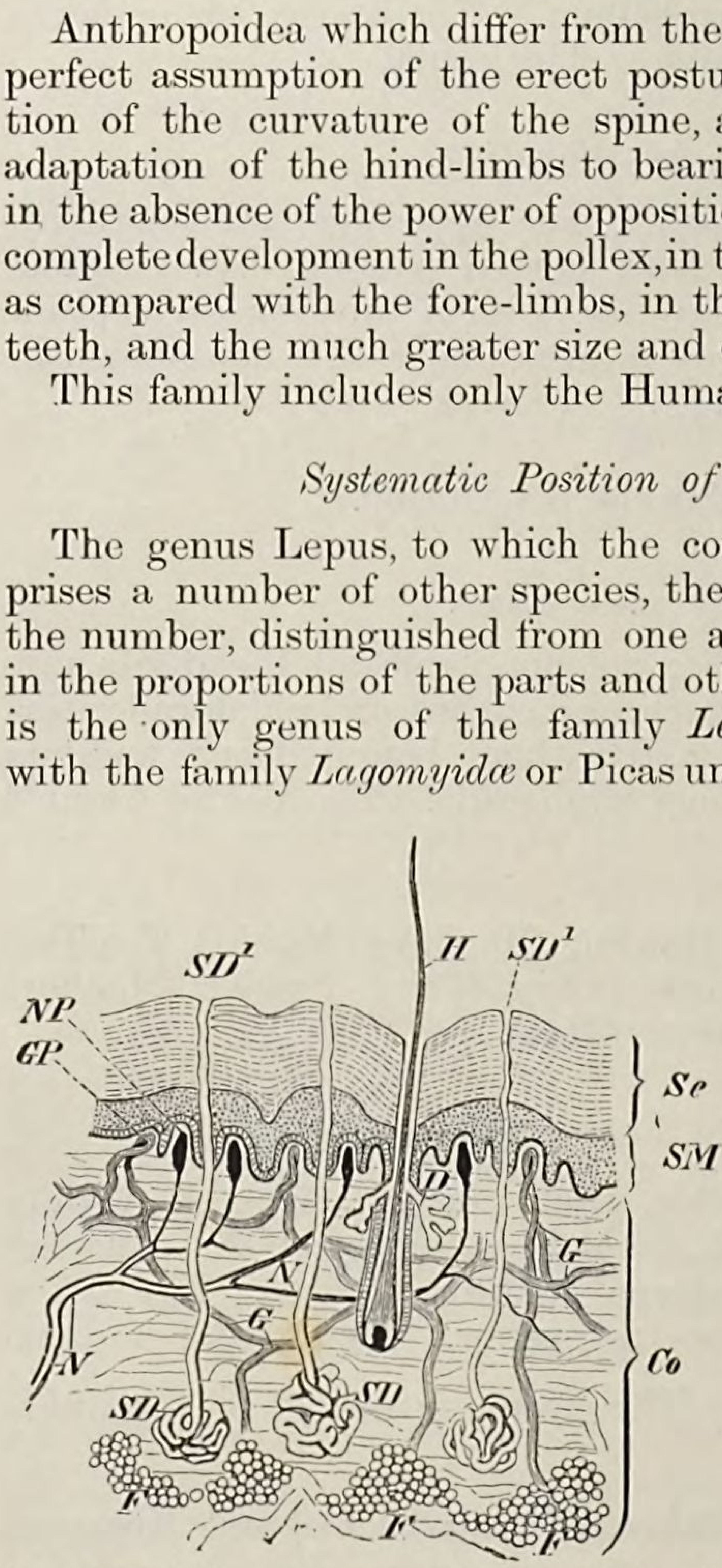


Fig. 1037.—Section of human skin. *Co*, dermis; *D*, sebaceous glands; *F*, fat in dermis; *G*, vessels in dermis; *GP*, vascular papillæ; *H*. hair; *N*. nerves in dermis; *NP*. nervous papillæ; *Se*, horny layer of epidermis; *SD*, sweat gland; *SD'*, duct of sweat gland; *SM*, Malpighian layer. (From Wiedersheim's *Comparative Anatomy*.)

3. General Organisation.

Integument and General External Features.—Nearly all Mammals are covered with *hairs* (Fig. 1037) developed in *hair-follicles.* Each hair (Fig. 1038) is a slender

rod, and is composed of two parts, a central part or *pith* (*M*) containing air, and an outer more solid part or *cortex* (*R*) in which air does not occur. Commonly the cortical part presents transverse ridges so as to appear scaly. In one case only, viz., Sloths, is the hair fluted longitudinally. The presence of processes on the surface, by which the hairs when twisted together interlock firmly, gives a special quality to certain kinds of hair—wool—used for clothing, the *felting* quality as it is termed. A hair is usually cylindrical; but there are many exceptions: in some it is compressed at the extremity, in others it is compressed throughout; the latter condition is observable in the hair of negroid races of men. The fur is usually composed entirely of one kind of hair; but in some cases there are two kinds, the hairs of the one sort very numerous and forming the soft fur, and those of the other consisting of longer and coarser hairs scattered over the surface. An example of a hairy covering of this kind is seen in the case of the Platypus and the Fur Seals.

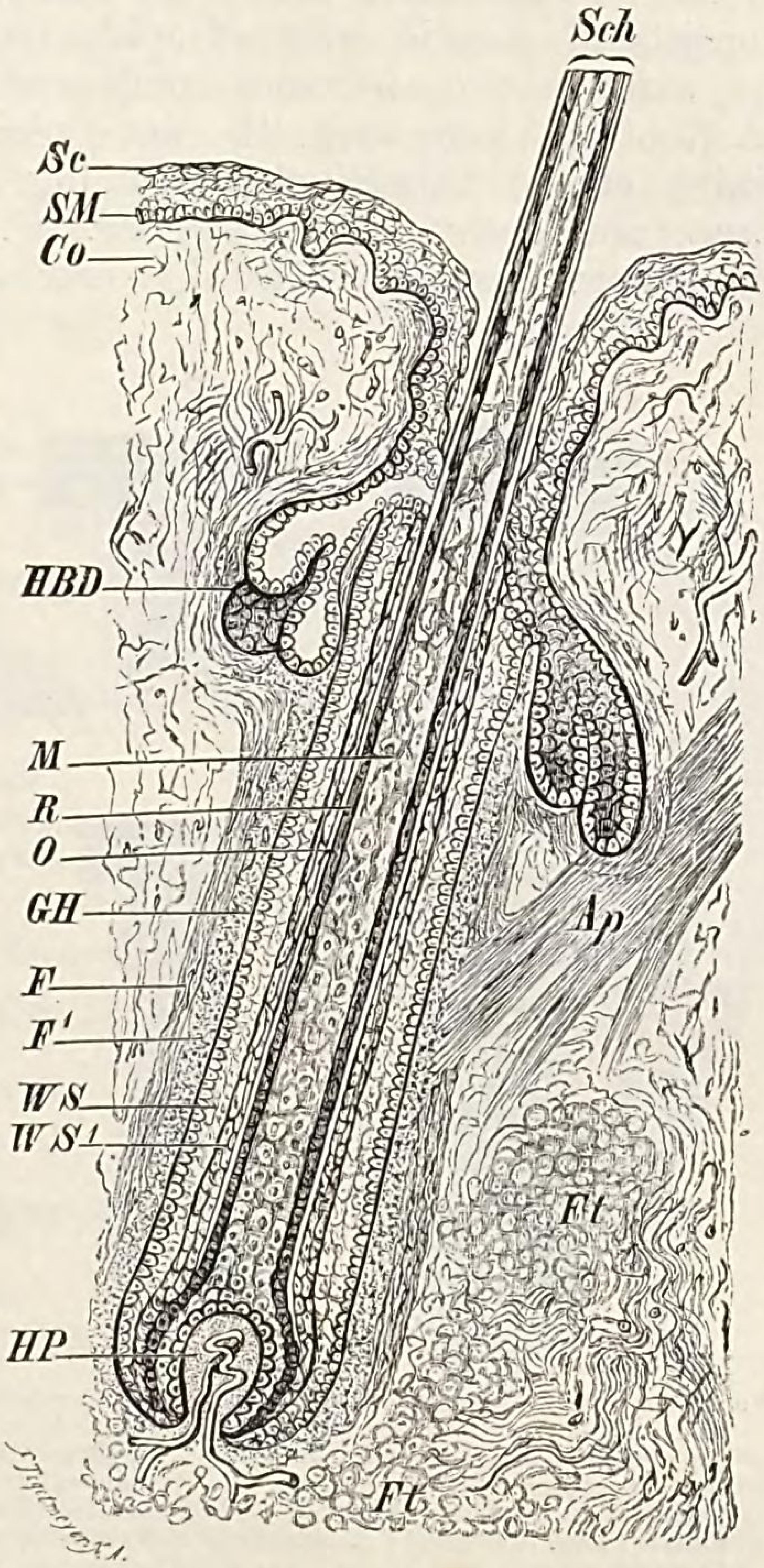


FIG. 1038.—Longitudinal section through a hair (diagrammatic). *Ap*, band of muscular fibres inserted into the hair follicle; *Co.* corium (dermis); *F.* external longitudinal; *F'.* internal circular fibrous layer of follicle; *Ft*, fatty tissue in the dermis; *GH*, hyaline membrane between the root-sheath and the follicle; *HBD*, sebaceous gland; *HP.* hair papilla with vessels in its interior; *M.* medullary substance (pith) of the hair; *R*, cortical layer; *Sc*, horny layer of epidermis; *SM*, Malpighian-layer of epidermis; *WS*, *WS'*, outer and inner layers of root-sheath. (From Wiedersheim's *Comparative Anatomy*.)

A hair, like a feather, is formed from the epidermis. The first rudiment of a developing hair (Fig. 1039) usually takes the form of a slight downwardly projecting outgrowth, the *hair germ* (*grm.*), from the lower mucous layer of the epidermis, beneath which there is soon discernible

a condensation of the dermal tissue to form the rudiment of a *hair papilla* (*pp.*). In some Mammals, however, the dermal papilla makes its appearance before the hair germ. The hair germ, which consists of a solid mass of epidermal cells, elongates, and soon its axial portion becomes condensed and cornified to form the shaft of the hair, while the more peripheral cells go to form the lining of the hair-follicle, becoming arranged in two layers, the *inner* and *outer root sheaths* ($sh^1.$, $sh^2.$). The epidermal cells in immediate contact with the hair papilla retain their protoplasmic character and form the *hair-bulb* (*blb.*), by the activity of which the further growth of the hair is effected. Soon the upper end of the hair shaft grows out beyond the surface of the epidermis, and the projecting part eventually becomes much longer than that which lies imbedded in the follicle. At the same time the follicle grows downwards into the dermis. During its growth the hair is nourished by the blood-vessels in the dermal hair-papilla, which projects into its base.

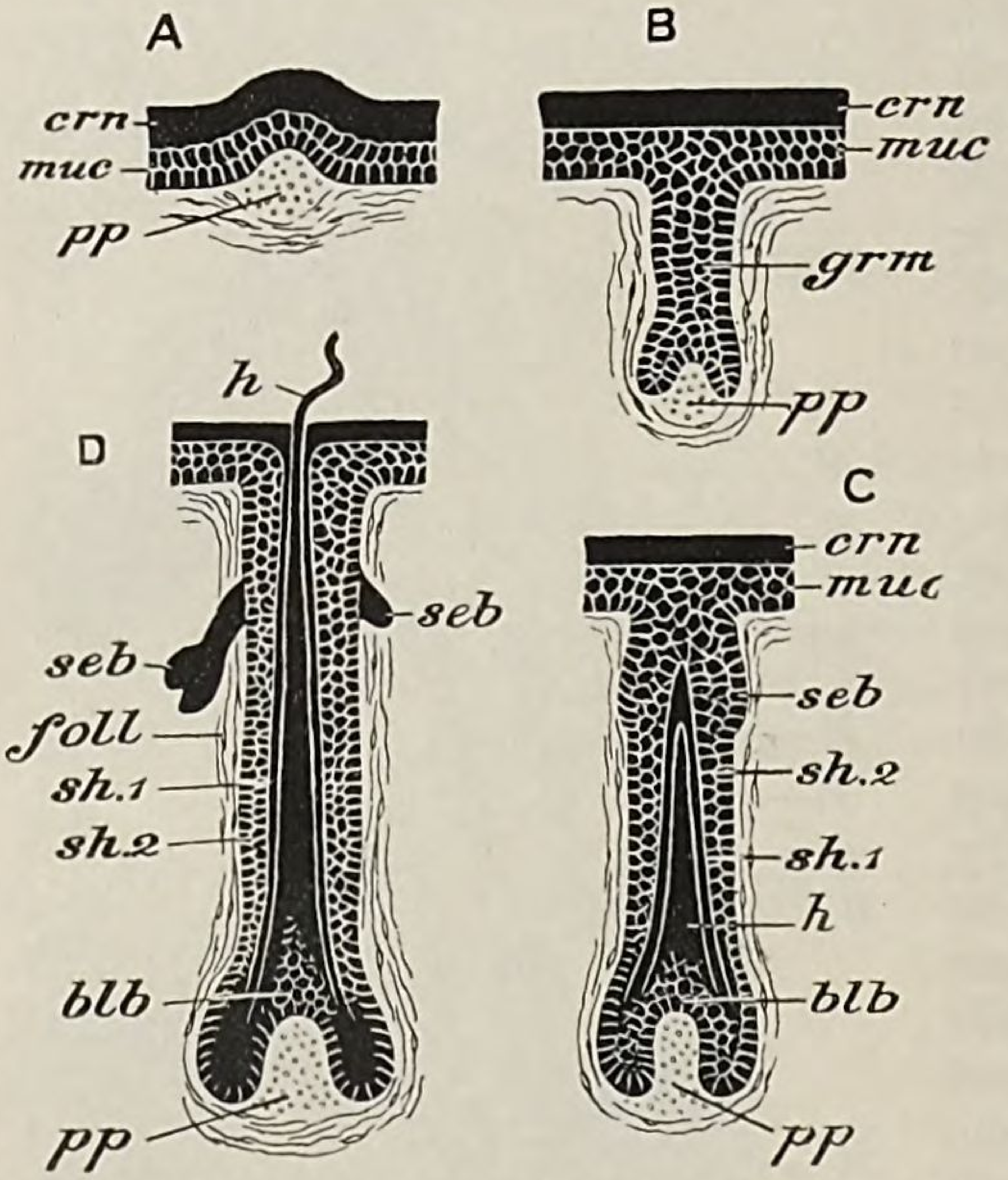


FIG. 1039.—Four diagrams of stages in the development of a hair. *A*, earliest stage in one of those Mammals in which the dermal papilla appears first; *B*, *C*, *D*, three stages in the development of the hair in the human embryo. *blb.* hair-bulb; *crn*, horny layer of the epidermis; *foll.* hair-follicle; *grm.* hair-germ; *h.* extremity of hair projecting on the surface; *muc.* Malpighian layer of epidermis; *pp.* dermal papilla; *seb.* developing sebaceous glands; sh^1. sh^2. inner and outer root-sheaths. (After Hertwig.)

Modifications of the hairs are often found in certain parts. Such modified hairs are the elongated hairs of the tails of some Mammals, *e.g.*, most Ungulates; the eye-lashes of the eye-lids, which are stronger than the ordinary hairs; and sensitive hairs or *vibrissæ* about the snout. In some Mammals the hairs in part assume the form of spines, viz., in Echidna, the Hedgehogs, and the Porcupines.

The coating of hairs is scanty in some Mammals, and is virtually absent in the Cetacea and Sirenia. In such cases the skin is greatly thickened, as in the Elephants, &c., or, as in the

Cetacea, an underlying layer of fat performs the function of the hairs as a heat-preserving covering.

In Manis (Fig. 1050) the greater part of the surface is covered with large rounded overlapping horny scales of epidermal origin, similar in their mode of development to those of Reptiles. A similar phenomenon is seen in the integument of the tail of *Anomalurus*—a Flying Rodent. The Armadillo is the only Mammal in which there occurs a bony *dermal exoskeleton* (*vide infra*).

Also epidermal in their origin are the horny structures in the form of nails, claws, or hoofs, with which the terminations of the

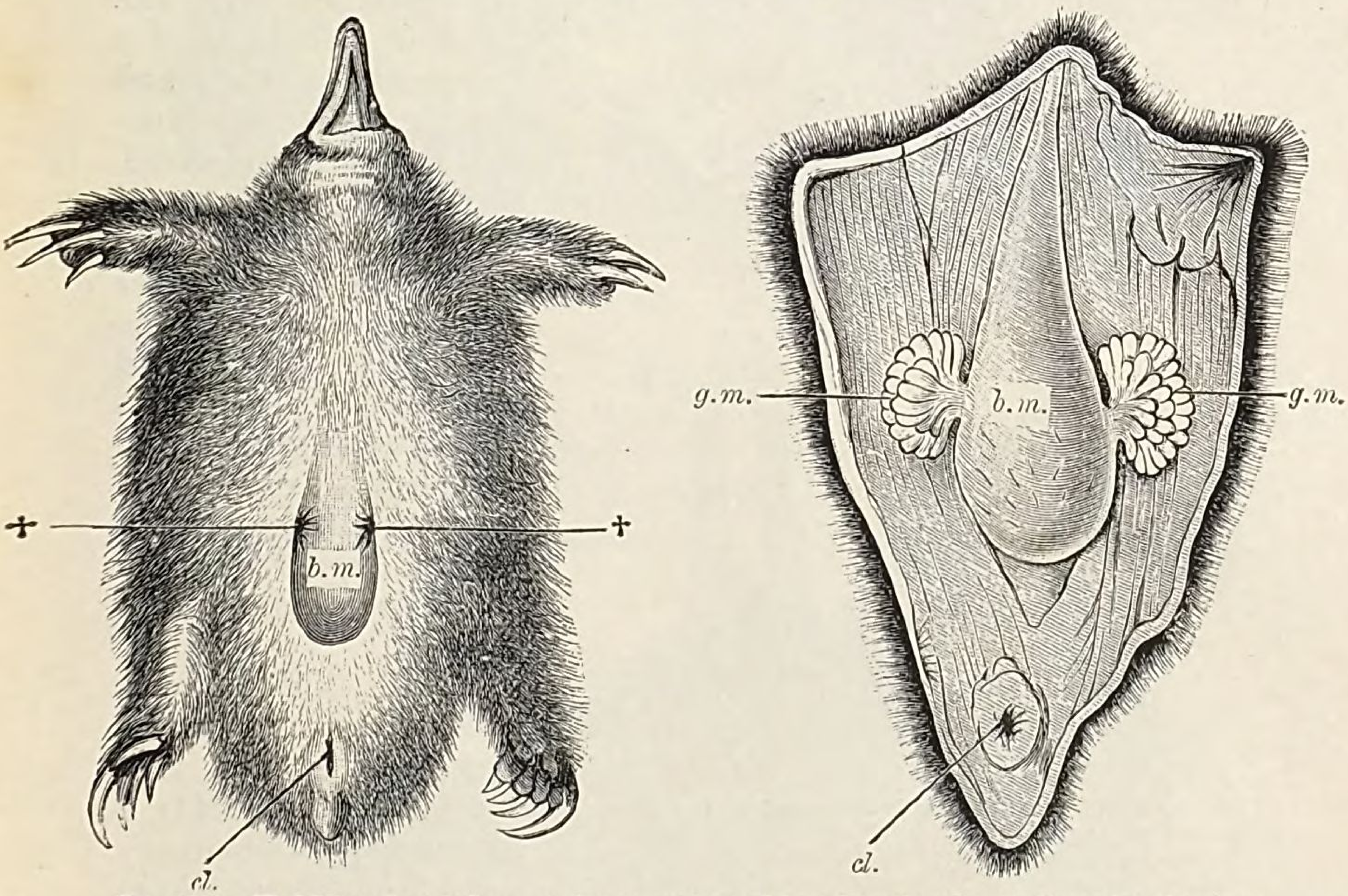


FIG. 1040.—**Echidna hystrix.** *A*, lower surface of brooding female; *B*, dissection showing a dorsal view of the pouch and mammary glands; † †, the two tufts of hair in the lateral folds of the mammary pouch from which the secretion flows; *bm*, pouch; *cl.* cloaca; *g. m.* groups of mammary glands. (From Wiedersheim's *Comparative Anatomy*, after W. Haacke.)

digits are provided in all the Mammalia except the Cetacea. And the same holds good of the horny portion of the *horns* of Ruminants. The horns of the Rhinoceros are also epidermal, and have the appearance of being formed by the agglutination of a number of hair-like horny fibres.

Cutaneous glands are very general in the Mammalia, the most constant being the *sebaceous glands* (Figs. 1037, *D*; 1038, *H, B, D*), which open into the hair-follicles, and the *sweat glands* (Fig. 1037, *SD*). In many Mammals there are, in addition, in various parts of the body, aggregations of special glands secreting an odorous matter.

The *mammary glands*, by the secretion of which the young are nourished, are specially developed cutaneous glands.

The mammary glands of the Prototheria differ from those of other Mammals in the absence of teats. They consist of two groups of very large tubular follicles, the ducts of which open on the ventral surface. In Echidna (Fig. 1040) the two areas on which the ducts open become depressed towards the breeding season to give rise to a pair of pouches—the mammary pouches. At a later period the part of the body-wall on which these mammary pouches are situated becomes modified to form a marsupium or pouch in which the mammary areas are contained. In this, which is of a temporary nature and disappears after its function has been performed, the egg is deposited when laid, and in this the young animal, after it has escaped from the egg, is protected and nourished. In Ornithorhynchus mammary pouches are indicated only by extremely shallow depressions, and no marsupium is developed.

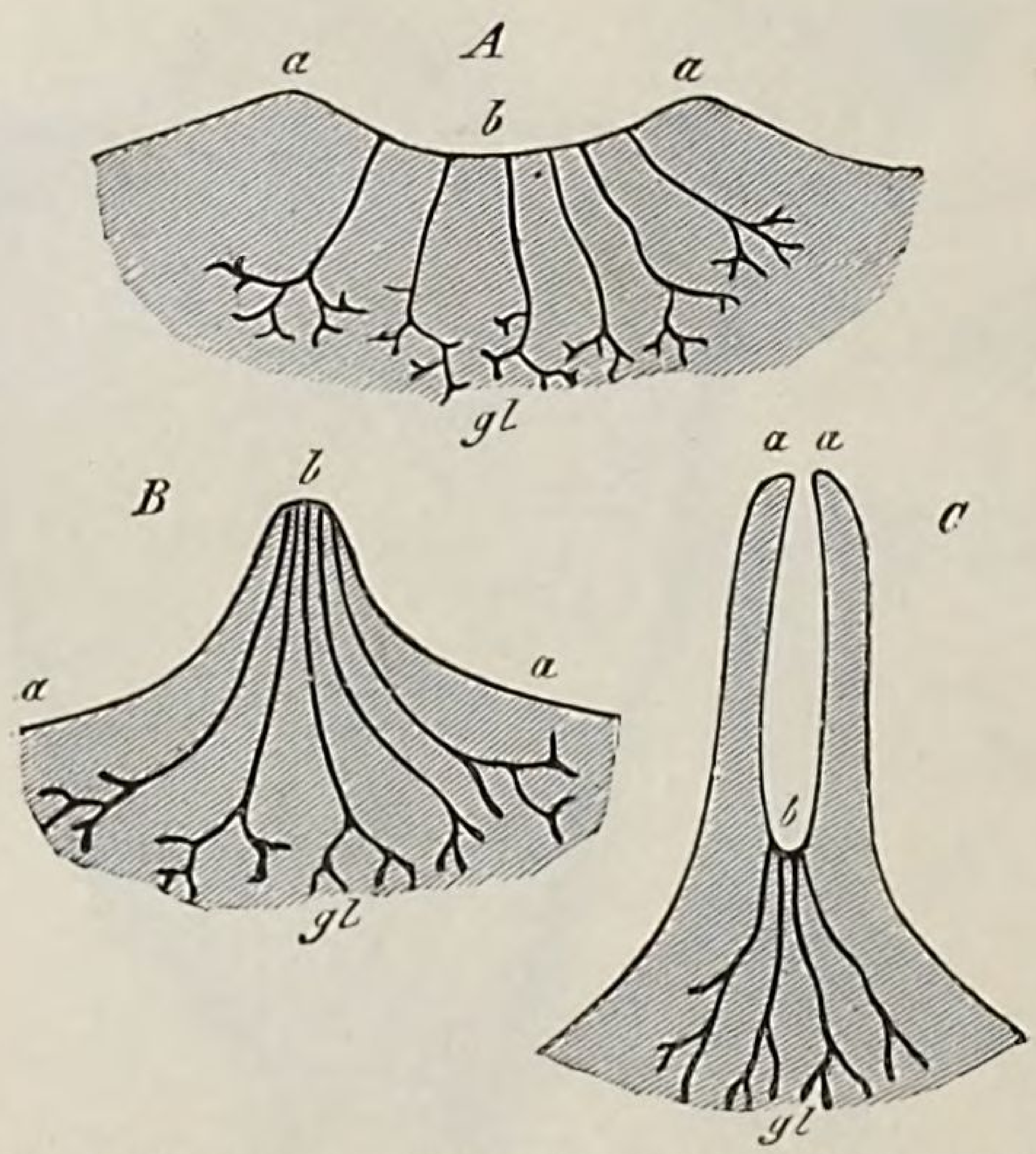


FIG. 1041.—Diagram of the development of the nipple (vertical section). *A*, indifferent stage, glandular area flat; *B*, elevation of the glandular area with the nipple; *C*, elevation of the periphery of the glandular area into the false teat. *a*, periphery of the glandular area; *b*, glandular area; *gl*. glands. (From Gegenbaur.)

In the higher Mammals, when the mammary glands are first developed (Fig. 1041), a depression (*mammary pouch*) is formed, from the floor of which branching cylindrical strands of epidermis grow inwards to give rise to the glands. In some cases (Marsupials, Primates) the mammary pouch disappears, and the area on which the glands open is raised up into a conical prominence—the *teat*. In the rest the edges of the mammary pouch grow upwards to form a prominence—the *false teat* (*C*)—with a central canal, into which, at the base, the ducts of the glands open. The number and situation of the true or false teats varies in the different groups, and has been noticed in the synopsis of the characters of the orders and sub-orders (pp. 450 to 460).

The two genera of the Prototheria, *Ornithorhynchus* and *Echidna*, differ somewhat widely from one another in general appearance.

The former (Fig. 1042) has the surface covered with a close, soft fur, and has the upper jaw produced into a depressed muzzle, not unlike the beak of a duck, covered with a smooth, hairless



FIG. 1042.—**Duck-Bill** (*Ornithorhynchus anatinus*). (After Vogt and Specht.)

integument, which forms a free fold or flap at the base. The eyes are very small, and there is no auditory pinna. The legs are short, and the five digits end in strong claws, and are connected together by a web, so that the limbs are equally adapted for burrowing and for swimming. The tail is elongated and



FIG. 1043.—**Spiny Ant-Eater** (*Echidna aculeata*). (After Vogt and Specht.)

depressed, and is covered with fur. The male has a sharp-pointed, curved spur on the inner side of the foot, having the duct of a poison-gland opening at its apex. Echidna (Fig. 1043) has the body covered above with strong pointed spines, between which are coarse hairs; the lower surface is covered with hair

only. The jaws are produced into a rostrum, which is much narrower than that of Ornithorhynchus. The eyes are small, and there is no auditory pinna. The limbs are short and powerful. There are five toes on each foot, each ending in a very strong claw, by means of which the Echidna is able to burrow with rapidity. The tail is vestigial.



FIG. 1044.—**Virginian Opossum** (*Didelphys virginiana*). (After Vogt and Specht.)

The Opossums (*Didelphyidæ*) (Fig. 1044) are arboreal rat-like Marsupials, with elongated naked muzzle, with well-developed, though nailless, opposable hallux, and elongated prehensile tail. A marsupium is sometimes present, but is absent or incomplete in the majority. One species—the Water Opossum—has the toes webbed. The Dasyuridæ (Australian Native Cats, Tasmanian Devil, Thylacine, etc.) have the pollex often rudimentary, the foot four-toed, the hallux, when present, small and clawless, and the tail not prehensile.



FIG. 1045.—**Dasyure** (*Dasyurus viverrinus*). (After Vogt and Specht.)

There is a well-developed marsupium. The Native Cats (Fig. 1045) and their near allies are cat-like animals, the largest equal in size to a Domestic Cat, some no larger than Rats or Mice; the Tasmanian Devil is of more thickset body; the Thylacine has a remarkable resemblance in general shape, as well as size, to a Wolf. The Banded Anteater (*Myrmecobius*) is devoid of the marsupium.



FIG. 1046.—**Rock Wallaby** (*Petrogale xanthopus*). (After Vogt and Specht.)

The Bandicoots (*Peramelidæ*) are burrowing Marsupials, the size of which varies from that of a large Rat to that of a Rabbit. They have an elongated pointed muzzle, and, in some cases, large auditory pinnæ. The tail is usually short, sometimes long. The first and fifth digits of the fore-feet are vestigial or absent, the remaining three nearly equally developed. In the hind-foot the fourth toe is much longer and stouter than the others, while the second and third are small and slender, and united together by a web of skin, and the first is vestigial or absent. The marsupium has its opening directed backwards.

Notoryctes, the Marsupial Mole, is a small burrowing Marsupial, with short and powerful limbs, each with five toes, the third and fourth toes of the fore-foot provided with remarkable, large, flat, triangular claws. The tail is short, and covered with bare skin. An auditory pinna is absent and the eyes are vestigial. The pouch opens backwards.

The Wombats (*Phascolomyidæ*) are large, heavy, thick-bodied, burrowing animals, with short flattened heads, short thick limbs, provided with strong claws on all the digits except the hallux, and

with the second, third and fourth of the hind-foot partly connected together by skin. The tail is very short. The Kangaroos and their allies (Macropodidæ) (Fig. 1046) are adapted, as regards their limbs, for swift terrestrial locomotion. They have a relatively small head and neck, the fore-limbs small, and each provided with five digits; the hind legs long and powerful; rapid progression is effected by great springing leaps, with the body inclined forwards and the fore-limbs clear of the ground. The foot is narrow and provided with four toes, the hallux being absent; the two inner (second and third) small and united together by integument, while the middle one is very long and powerful. The tail is very long, and usually thick. There is a large marsupium. The Tree-Kangaroos differ from the ordinary Kangaroos in their shorter and thicker hind-limbs, in which the second and third toes are nearly as large as the fourth.

The Phalangers (*Phalangeridæ*) are climbing Marsupials which have both fore- and hind-feet prehensile; the second and third toes of the hind-foot slender and united by a web, as in the



FIG. 1047.—**Koala** (*Phascolarctos cinereus*). (After Vogt and Specht.)

Kangaroo, but the hallux, which is nailless, opposable to them; the fourth and fifth nearly equal; the tail is well developed and prehensile. A number of Phalangers (Flying Phalangers) are provided with lateral folds of skin extending from the fore- to the hind-limbs and, acting as a parachute, enabling the animal, as in the Flying Squirrels, to perform flying leaps from tree to tree. The Koalas (Fig. 1047) differ from the Phalangers mainly in the relatively thicker body and the vestigial tail.

The Sloths (*Bradypodidæ*) (Fig. 1048) are more completely

adapted, in the structure of their limbs, to an arboreal life than any other group of the Mammalia. They have a short, rounded head, with small pinnæ, and long slender limbs, the anterior much longer than the posterior, with the digits, which are never more than three in number, long, curved, and hook-like, adapted for enabling the animal to hang and climb, body downwards, among the branches of trees. In the three-toed Sloth there are three toes in both manus and pes; in the two-toed Sloth there are only two in the manus, three in the pes. The tail is rudimentary. The body is covered with long, coarse hairs, which differ from those of other Mammals in being longitudinally fluted. On these hairs grows abundantly an alga, the presence of which gives a greenish tinge to the fur.



FIG. 1048.—**Unau,** or **Two-Toed Sloth** (*Cholœpus didactylus*). (After Vogt and Specht.)

The ordinary Anteaters (*Myrmecophaga*) have a greatly elongated snout, with the mouth as a small aperture at its extremity, small eyes, and the auditory pinna sometimes small, sometimes well developed. There are five digits in the fore-foot, of which the third has always a very large, curved and pointed claw, rendering the manus an efficient digging organ. The toes of the hind-foot, four or five in number, are sub-equal, and provided with moderate-sized claws. In walking, the weight of the body rests on the dorsal surfaces of the second, third and fourth digits of the manus, and on a thick callous pad on the extremity of the fifth, and, in the pes, on the entire plantar surface. The tail is always very long, and is sometimes prehensile. The body is covered with long hair. In the Two-toed Anteater (*Cycloturus*) the muzzle is

short; there are four toes in the manus, of which the second and third only have claws, that of the third being the longer; the pes has four sub-equal clawed toes, forming a hook not unlike the foot of the Sloths; and the tail is prehensile.

In the Armadillos (*Dasypodidæ*) (Fig. 1049) the head is comparatively short, broad and depressed. The number of complete

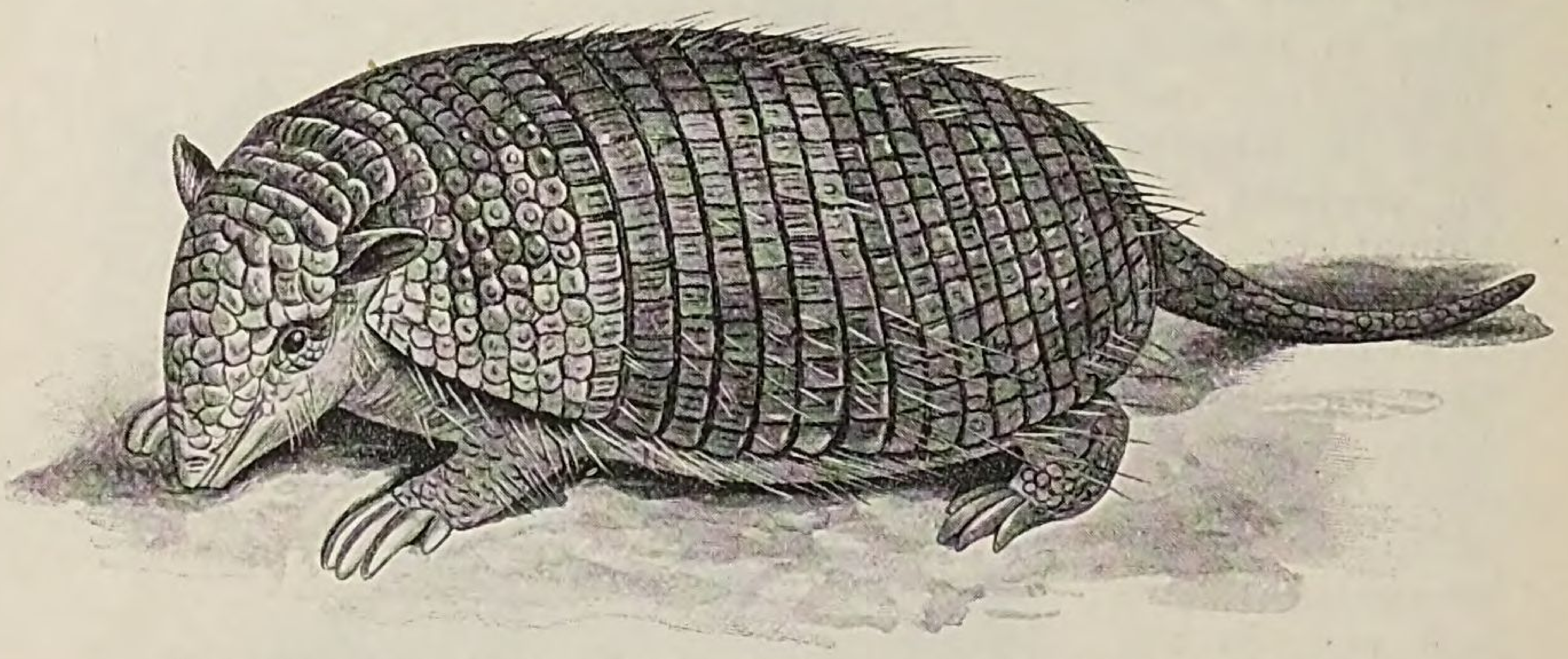


FIG. 1049.—**Tatu Armadillo** (*Dasypus sexcinctus*). (After Vogt and Specht.)

digits of the fore-foot varies from three to five; these are provided with powerful claws, so as to form a very efficient digging organ. The hind-foot always has five digits with smaller claws. The tail is usually well developed. The most striking external feature of the Armadillos is the presence of an armour of bony dermal plates. This usually consists of a scapular shield of closely-united plates covering the anterior part of the body, followed by a series of transverse bands separated from one another by hairy skin, and a posterior pelvic shield. Sometimes these bands are movable, so that the animal is enabled to roll itself up into a ball. The tail is also usually enclosed in rings of bony plates, and a number protect the upper surface of the head.

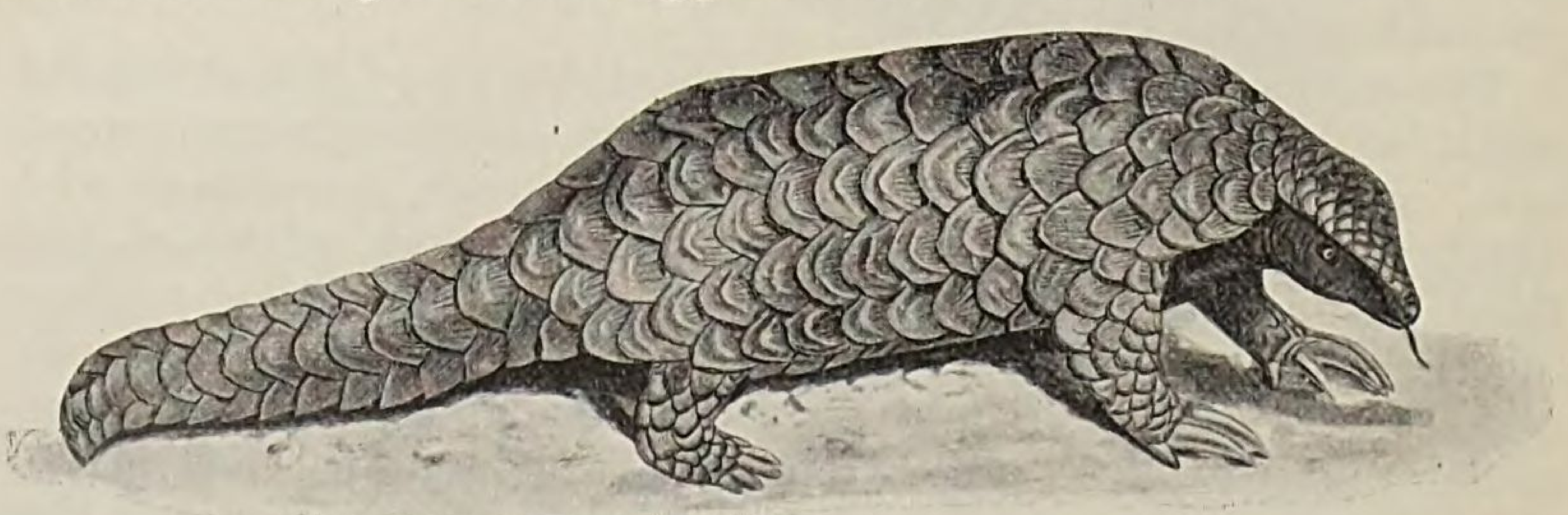


FIG. 1050.—**Scaly Anteater** (*Manis pentadactyla*). (After Vogt and Specht.)

In the Scaly Anteaters (*Manis*) (Fig. 1050) the head is produced into a short pointed muzzle. The limbs are short and strong, with

five digits in each foot. The upper surface of the head and body, the sides of the latter, and the entire surface of the tail, are covered with an investment of rounded horny epidermal scales. The lower surface is covered with hair, and there are a few coarse hairs between the scales. There are five digits in both manus and pes. In walking the weight rests on the upper and outer side of the fourth and fifth toes of the manus, and on the sole of the pes.

The Aard-varks (Fig. 1051) have a thick-set body, the head produced into a long muzzle with a small tubular mouth, the pinnæ of great length, the tail long and thick. The fore-limbs are short and stout, with four toes, the palmar surfaces of which

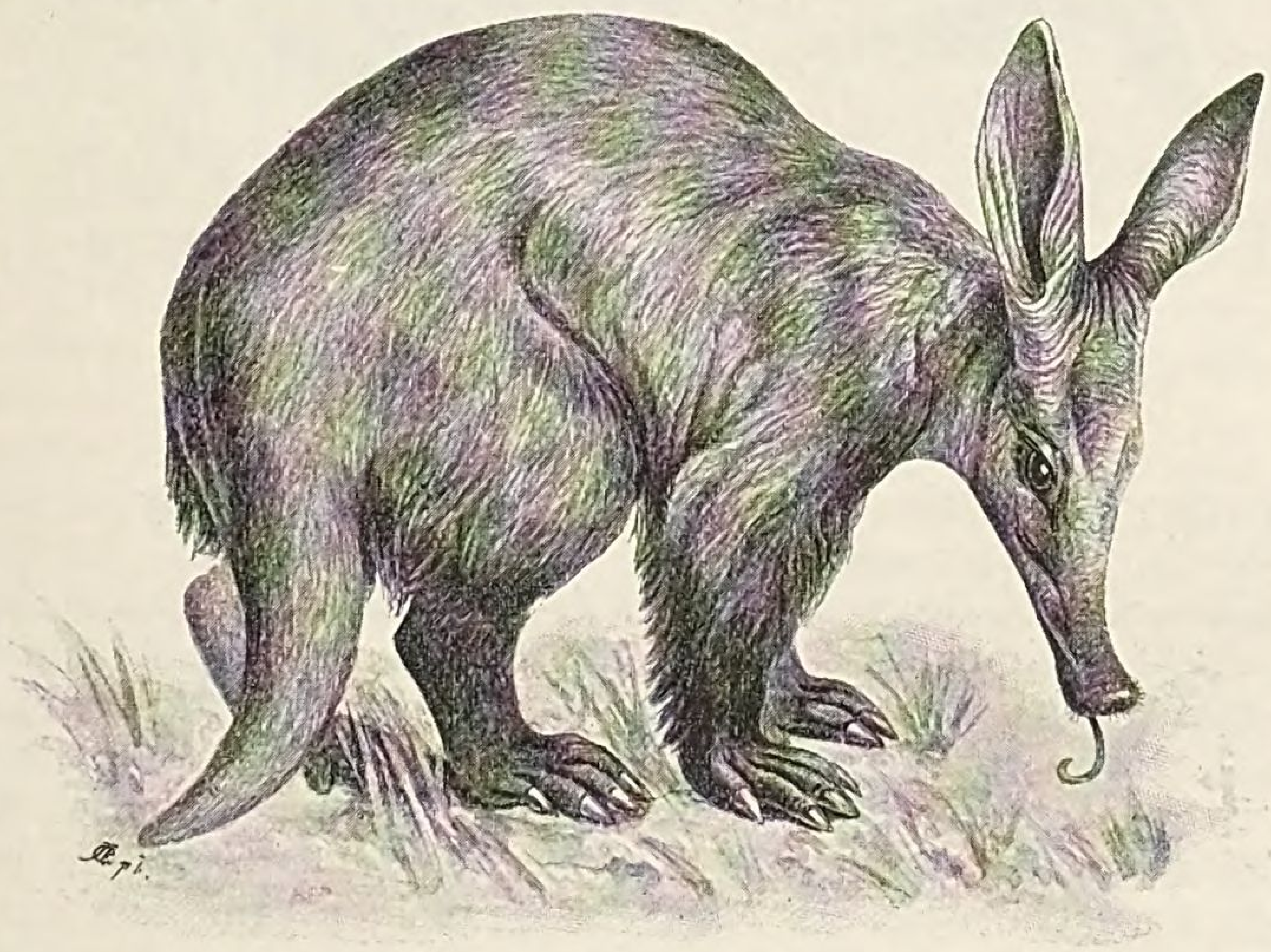


FIG. 1051.—**Aard Vark** (*Orycteropus capensis*). (After Vogt and Specht.)

are placed on the ground in walking. The hind-limb is five-toed. The surface is covered with thick skin with sparse hairs.

The Cetacea (Fig. 1052), among which are the largest of existing Mammals, are characterised by the possession of a fusiform, fish-like body, tapering backwards to the tail, which is provided with a horizontally expanded caudal fin divided into two lobes or "flukes," and a relatively large head, not separated from the body by any distinct neck. A dorsal median fin is usually present. The fore-limbs take the form of flippers, with the digits covered over by a common integument, and devoid of claws; the hind-limbs are absent. The mouth is very wide; the nostrils are situated on the summit of the head, and the auditory pinna is absent. Hairs are completely absent, or are

represented only by a few bristles about the mouth. In the Whale-bone Whales the nostrils have two external slit-like apertures; in the Toothed Whales, Porpoises, and Dolphins, on

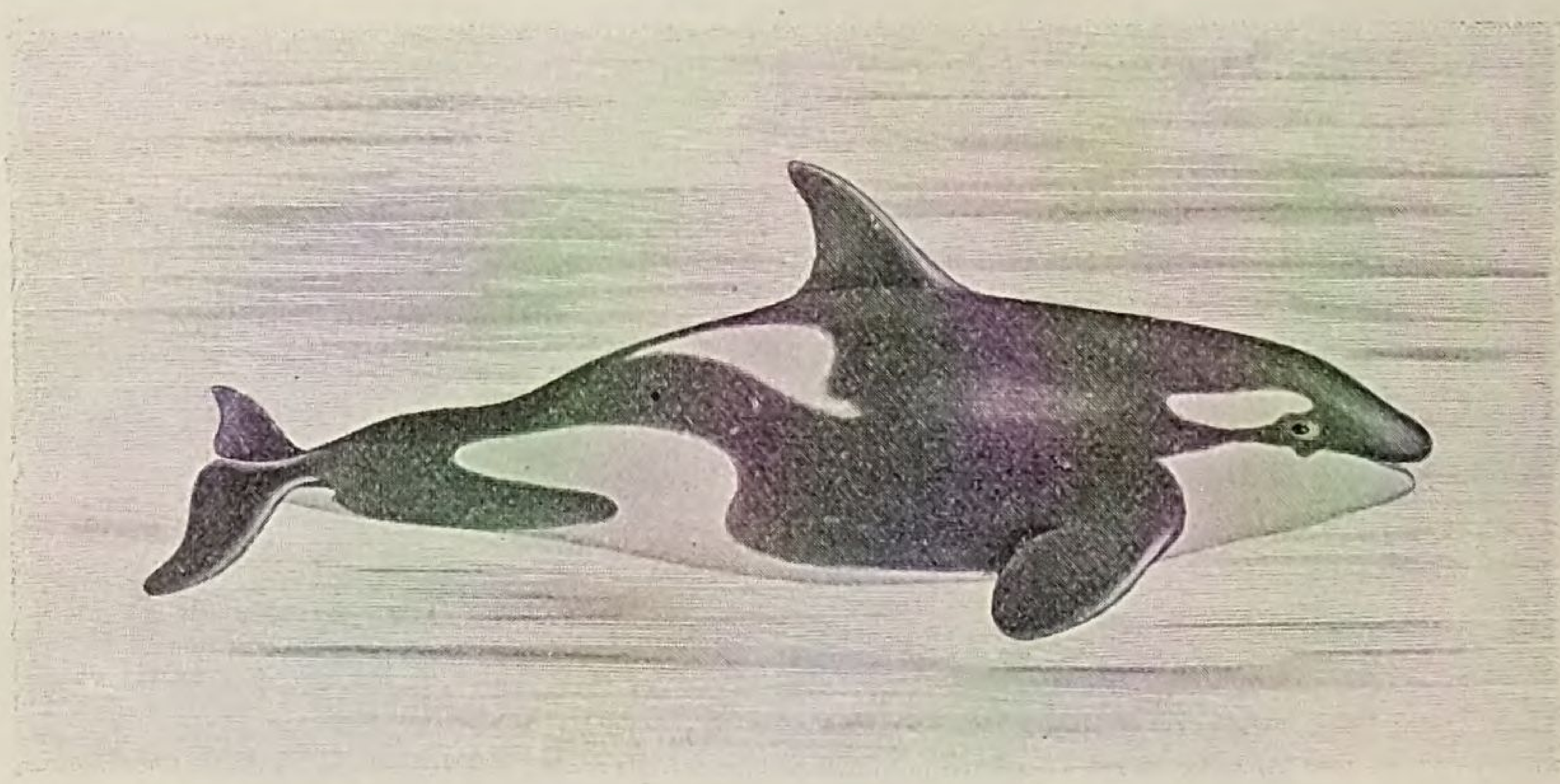


FIG. 1052.—**Killer** (*Orca gladiator*). (After True.)

the other hand, the two nostrils unite to open by a single crescentic valvular aperture.

In the Sirenia also the body is fish-like, with a horizontal caudal fin, the fore-limbs flipper-like, the hind-limbs absent, and the integument almost hairless. But the body is distinctly depressed, and the head is by no means so large in proportion as in the Cetacea, and has a tumid truncated muzzle, not far back from the extremity of which the nostrils are situated. There is no dorsal fin. The eyes are small, the pinnæ of the ears absent. The digits are in some cases provided with claws.

In the Ungulata vera the claws or nails of other Mammals are replaced by thick solid masses, the *hoofs*, investing the ungual phalanges and bearing the weight of the body. The number of digits is more or less reduced, and the limbs as a whole are usually specially modified to act as organs of swift locomotion over the surface of the ground, their movements being restricted, by the nature of the articulations, to antero-posterior movements of flexion and extension. The metacarpal and metatarsal regions are relatively very long. In the Artiodactyla the third and fourth digits of each foot form a symmetrical pair. In the Ruminants vestiges of the second and fifth digits are also commonly present; but these are usually not functional, never reaching the ground, though in the Reindeer they are better developed than in the others, and have the effect of preventing the foot from so readily sinking in the snow. In the Camels the third and fourth digits

alone are present. The Giraffes are distinguished from the other Ruminants by the enormous length of the neck. Characteristic of the Ruminants, though absent in the Camels and some others, are the cephalic appendages known as *horns* and *antlers*. The horns of the Hollow-horned Ruminants (Oxen, Sheep, Goats, Antelopes) sometimes developed in both sexes, sometimes only in the males, are horny sheaths supported on bony cores, which are outgrowths of the frontal bones. In the Giraffes the horns, which are short and occur in both sexes, are bony structures covered with soft skin, and not at first attached by bony union to the skull, though subsequently becoming firmly fixed. Between them is a short rounded median bony protuberance on the frontal region of the skull. The antlers of the Deer, which, except in the case of the Reindeer, are restricted to the male sex, are bony growths enclosed only while immature in a layer of skin, the "velvet," covered with very soft short fur. Antlers are shed annually, and renewed by the growth of fresh vascular bony tissue from the summit of a pair of short processes of the frontal bones, the *pedicles*. Eventually when the antlers are fully grown, a ring-like thickening of the bone, the "burr," appears round the base of the antler, and constricts the blood-vessels, so that the substance of the antler becomes converted into dry dead bone; the skin shrivels and is peeled off. The antler is shed by the absorption of the bone immediately beneath the burr. The pinnæ of the ear of the Ruminants are well-developed. The tail is sometimes elongated, and provided with a terminal leash of long coarse hairs; sometimes short and bushy. The entire surface, with the exception of the end of the muzzle, which is naked, is always covered with a close coat of longer or shorter hairs.

In the Pigs the legs are relatively short, and the two lateral toes of both manus and pes are fully developed, though scarcely reaching the ground. The surface is covered with a scanty coat of coarse bristles. There is a truncate mobile snout, the anterior end of which is disc-shaped and free from hairs. The pinnæ are large; the tail is rather long, narrow, and cylindrical, provided with a terminal tuft of strong hairs. A remarkable feature of the males is the development of the canine teeth of both jaws into large, upwardly-curved tusks. In the Peccaries, which resemble the Pigs in most of the features mentioned, the points of the upper tusks are directed downwards.

In the Hippopotami the body is of great bulk, the limbs very short and thick, the head enormous, with a transversely expanded snout, prominent eyes, and small pinnæ. The tail is short and laterally compressed. The toes are four in each manus and pes, all reaching the ground. The surface is naked, with only a few hairs in certain positions; the skin is of great thickness.

In the Perissodactyles the third digit is either the only complete one in both fore- and hind-foot (Horses) or there are only three digits, second, third, and fourth in each (Rhinoceroses), or there are four in the fore-foot and three in the hind (Tapirs). The Horses (Equidæ) have the distal divisions of the limbs slender, the metacarpals and metatarsals nearly vertical to the surface of the ground; the single hoof massive and with a broad lower surface. Though the head is elongated, the nasal region is not produced into a proboscis. The tail is short or moderately long, and is either beset throughout with a large number of very long coarse hairs, or with a tuft of such specially developed hairs at the extremity. A mane of similar large hairs usually runs along the dorsal surface of the neck. There is a wart-like callosity above the wrist, and in the true Horses a second a little below the heel or "hock."

The Tapirs have the body more massive than the Horses, and the limbs, especially the distal segments, shorter and stouter. The nasal region is produced into a short proboscis. The surface is beset with a scanty covering of hairs. The tail is vestigial.

In the Rhinoceroses the body is extremely massive, the limbs short and stout, each digit provided with a hoof-like nail. There is a short soft muzzle. Either one or two remarkable median horns are borne on the nasal region, not attached directly to the skull: these are epidermal structures which are formed of a dense aggregation of slender fibre-like elements. The eyes are small, the auditory pinnæ well developed. The surface is devoid, or nearly devoid, of hairs, and the skin is enormously thick, and in some species thrown into deep folds. The tail is narrow and of moderate length.

The Hyraxes are small, somewhat Rabbit-like animals, with slender limbs and vestigial tail. There are four functional digits in the manus and three in the pes, all provided with short flat nails, except the innermost of the pes, which has a curved claw. The body is covered with soft fur.

The Elephants, the largest of existing terrestrial Mammals, have the limbs much more typically developed than in the true Ungulates, there being five comparatively short digits, enclosed in a common integument, in each foot, all of them in the fore- and three or four in the hind-foot terminating in a broad flat nail. The limbs are very stout and pillar-like, and the thigh and leg, when at rest, are in a straight line instead of being, as in the Ungulata vera, placed nearly at right angles to one another—a circumstance which gives a characteristic appearance to the hind-quarters. The nasal region is produced into a proboscis or "trunk," a mobile cylindrical appendage, longer than the rest of the head, at the extremity of which the nostrils are situated. There is in the male a pair of immense tusks—the incisors of

the upper jaw. The eyes are small, the pinnæ of the ears enormous. The tail is small. The skin is very thick, and provided with only a scanty hairy covering.

In the Carnivora the typical number of digits is sometimes present, or, more usually, there are five in the fore- and four in the hind-foot, or four in each. The extremities of the digits are provided with compressed curved claws, which may be very long and sharp, when they are capable, when not in use, of being retracted into a sheath of skin situated at their bases; or relatively short and blunt, when they are incompletely, or not at all, retractile. The Dogs (*Canidæ*) and Cats (*Felidæ*) are digitigrade, the Bears (*Ursidæ*) and allied groups plantigrade. The Otters (*Lutra*) differ from the rest in having short limbs with the toes connected by webs of skin.

The Pinnipedia (Fig. 1053) have the proximal segments of the limbs short, so that the arm and thigh, and nearly all the fore-arm

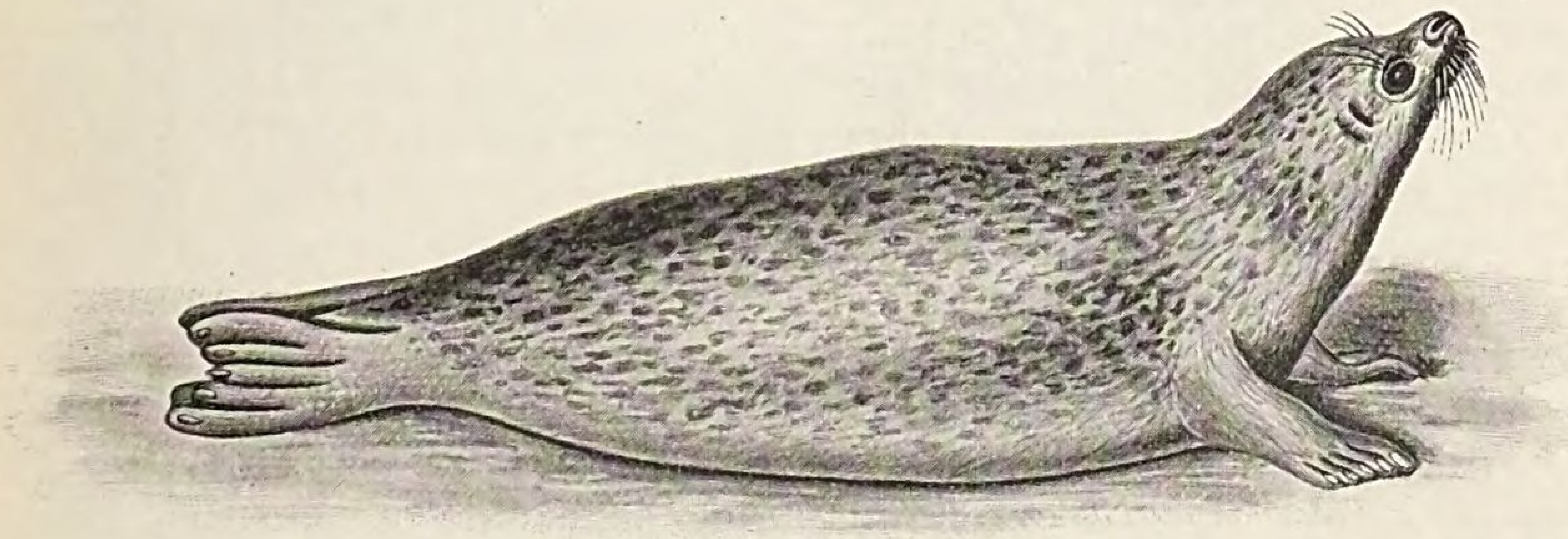


FIG. 1053.—**Seal** (*Phoca vitulina*).

and leg, are enclosed in the common integument of the trunk, and the manus and pes elongated. The Earless Seals (*Phocidæ*) are much more completely adapted to an aquatic life than the Eared Seals (*Otariidæ*) and Walruses (*Trichechidæ*), being unable to flex the thigh forwards under the body, so that the hind-limbs may aid in supporting the weight, and thus being only able to drag themselves along very awkwardly when on dry land. The pinna of the ear is absent in the Earless Seals and Walruses, well developed in the Eared Seals. The surface in all is covered with a thick soft fur. In the Fur Seals there are two kinds of hairs—those of the one kind being longer and coarser, and scattered through the more numerous shorter and finer hairs composing the fur proper. A remarkable feature of the Walruses is the presence of a pair of large tusks—the enlarged canine teeth—projecting downwards from the upper jaw.

Though some of the Rodents (Beavers, Water Voles) are aquatic, some (Squirrels and Tree-Porcupines) are arboreal, while others

(the majority of the order) lead a terrestrial life, and are active burrowers; they are on the whole a very uniform group, and exhibit few such remarkable modifications as are to be observed in some of the other orders of Mammals. They are nearly all furry animals with five-toed, plantigrade or semiplantigrade limbs. The tail is usually elongated, and may be naked or covered with fur; but sometimes, as in the Rabbits and Hares, it is very short. A few special modifications, however, have to be noted in certain families of Rodents. The Flying Squirrels have on each side a fold of skin, the patagium, which serves as a parachute. The African Flying Squirrels (*Anomalurus*) are remarkable also on account of the presence of a series of overlapping horny scales on the lower surface of the basal part of the tail. The Jerboas (*Dipus*) and their allies are characterised by the great relative length of the hind-limbs—the mode of locomotion of these remarkable Rodents being by a series of leaps not unlike the mode of progression of the Kangaroo—and by the reduction of the number of the toes to three in some of them. The Porcupines (*Hystricidæ*) have numerous elongated spines or "quills" among the hairs of the dorsal surface, and some of them have prehensile tails. The Agutis (*Dasyprocta*) have hoof-like claws, and the Capibara (*Hydrochœris*) has webs between the digits.

The Insectivora are, in general, small, furry, burrowing Mammals with plantigrade limbs and an elongated muzzle. But there is a considerable range of modification within the order in adaptation to different modes of life. The Colugos (*Galeopithecus*) (Fig. 1054) have a fold of skin extending along each side of the neck and body and continued between the hind legs, enclosing the tail, the fore-and hind-feet are both webbed, and the tail is prehensile. The Hedgehog (*Erinaceus*) has the surface beset with pointed spines. The Moles (*Talpa*) and their allies, which are active burrowers, have the limbs very short and stout and provided with extremely strong claws. The Jumping Shrews (*Macroscelididæ*) have slender limbs adapted to progressing by leaps on the surface of the ground.

The Chiroptera (Fig. 1055) are the only Mammals which are capable of active flight. The fore-limbs have the segments greatly elongated, especially the fore-arm and the four ulnar digits, and these support a thin fold of the integument which stretches to the hind-limbs and constitutes the wing. A fold also extends between the hind-limbs, and may or may not involve the tail. The pollex is much shorter than the other digits, is directed forwards, and terminates in a well developed curved claw; in the Megachiroptera, but not in the Microchiroptera, the second digit also has a claw; the other digits are always clawless. The position of the hind-limbs is peculiar, and the knee is directed backwards instead of forwards as in other Mammals; the five digits of the foot are all provided

with claws. So complete is the adaptation of the limbs to the purpose of flight that Bats are only able to shuffle along with

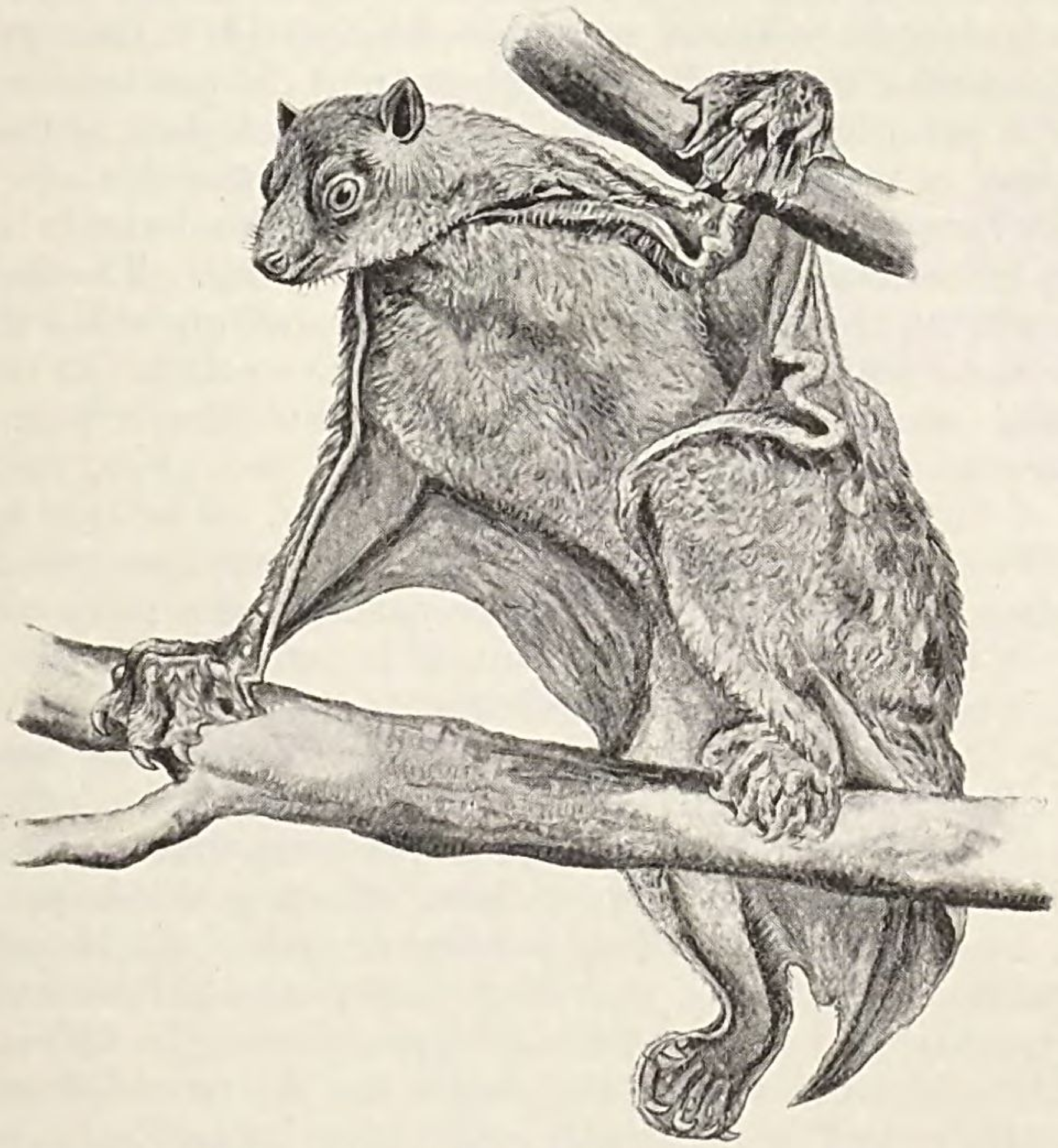


FIG. 1054.—**Galeopithecus.** (After Vogt and Specht.)

great difficulty on the ground; though with the aid of their claws they are able to climb and to suspend themselves from branches of trees by the hind feet. In the Megachiroptera the muzzle is

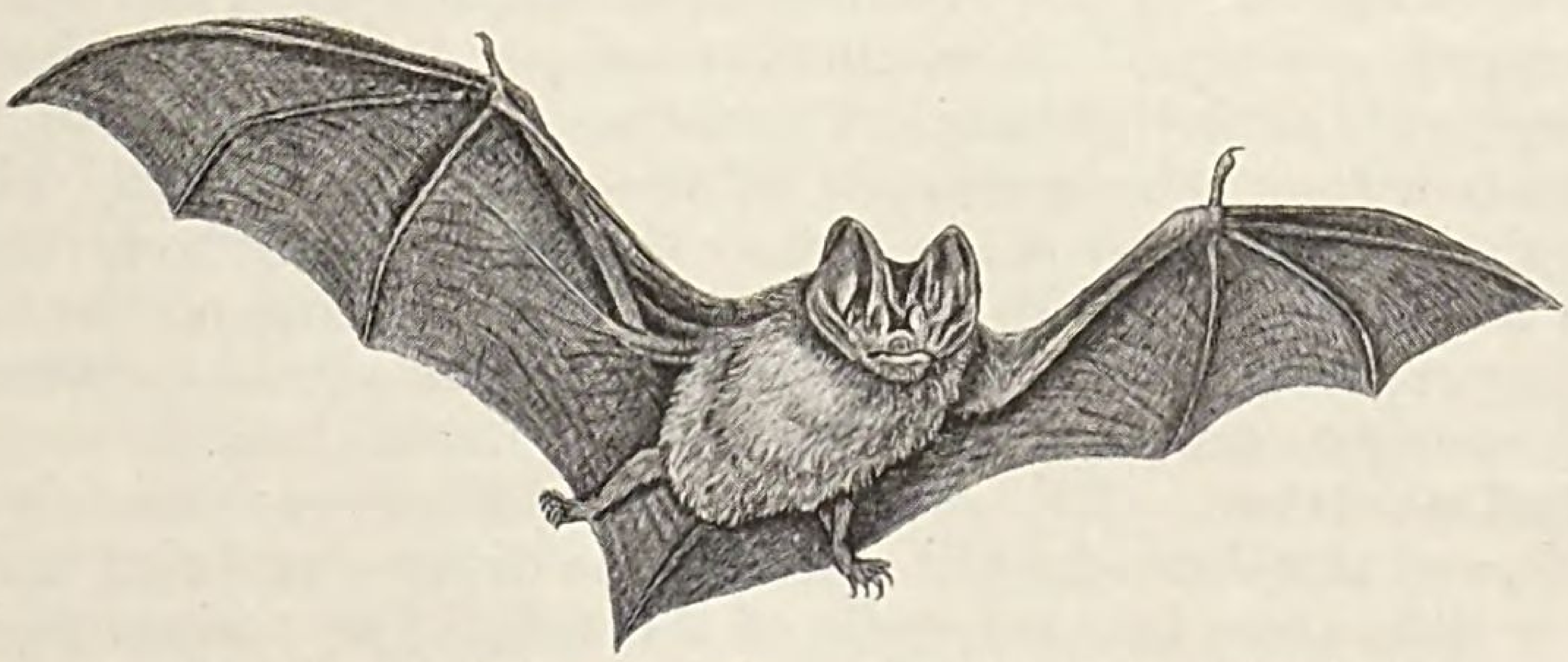


FIG. 1055.—**Bat** (*Synotus barbastellus*). (After Vogt and Specht.)

nearly always elongated, and the pinna of the ear simple, while in the Microchiroptera the muzzle is short, the pinna usually com-

plicated by the presence of an inner lobe or tragus, and often produced into remarkable arborescent appendages, and the nose also often provided with elaborate leaf-like or arborescent lobes. The surface is usually covered with soft fur, except in one group of Microchiroptera in which the integument is practically naked. The tail is sometimes short, sometimes well developed; in the latter case it may or may not be involved in the tail-membrane.

In the Lemurs and their allies (*Prosimii*) the body is slender, and the limbs adapted for an arboreal existence. The hallux is divergent from the other digits of the foot and opposable to them, and the same holds good, in some cases, of the pollex. In some, all the digits are provided with claws, or all but the hallux. More commonly all the digits are provided with flat nails, except the second of the pes, which always has a claw. The eyes are very large. The muzzle is sometimes elongated, sometimes short; the nostrils are slit-like. The tail is sometimes absent or short; more usually it is greatly elongated, but it is never prehensile. The surface is always covered with soft fur.

Of the Anthropoidea the Hapalidæ or Marmosets are small squirrel-like animals with all the digits except the hallux provided with pointed claws, with the pollex incapable of opposition, the tail non-prehensile, and without cheek-pouches or callous patches over the ischia. The Cebidæ resemble the Hapalidæ in the negative characters of the absence of ischial callosities and of cheek-pouches, and of the power of opposition in the hallux. But the limbs are much longer, the digits are all provided with flat nails, and the tail is frequently prehensile. The Cercopithecidæ all have brightly-coloured, bare, callous patches of skin (*callosities*) over the ischia, and most of them have cheek-pouches for the storage of food. All the digits are provided with flat nails. The tail may be long, or short, or absent; when present it is never prehensile. The pollex, when developed, is always opposable to the other digits. In the Simiidæ or Man-like Apes, a tail is never developed, and there are no cheek-pouches; ischial callosities are present only in the Gibbons. The Gibbons can walk in an upright position without the assistance of the fore-limbs; in the others, though, in progression on the surface of the ground, the body may be held in a semi-erect position with the weight resting on the hind-limbs, yet the assistance of the long fore-limbs acting as crutches is necessary to enable the animal to swing itself along.

Endoskeleton.—The spinal column of Mammals varies in the number of vertebræ which it contains, the differences being mainly due to differences in the length of the tail. The various regions are very definitely marked off. In the *cervical* region the first two vertebræ are modified to form the *atlas* and *axis*. Owing to the absence of distinct cervical ribs, the posterior cervical vertebræ are much more sharply marked off from the anterior thoracic than

is the case in Reptiles and Birds. The vertebræ of the cervical region have double transverse processes (or a transverse process perforated at the base by a foramen) in all except the last. The lower portion of the transverse process in certain cases (*e.g.*, seventh, and sometimes some of the others in Man) arises from a separate ossification, and this is regarded as evidence that the lower part, even when not independently ossified, represents a cervical rib. Seven is the prevailing number of vertebræ in the cervical region; there are only three exceptions to this—the Manatee, Hoffmann's Sloth, and the three-toed Sloth. The number of *thoracic* and *lumbar* vertebræ is not so constant; usually there are between nineteen and twenty-three. Hyrax has a larger number of thoracico-lumbar vertebræ than any other Mammal—from twenty-nine to thirty-one.

The thoracic vertebræ have *ribs* which are connected, either directly or by intermediate ribs, with the *sternal ribs*, and through them with the *sternum*. Each rib in general articulates with the spinal column by two articulations—one articular surface being borne on the head and the other on the tubercle. The tubercle articulates with the transverse process, and the head usually with an articular surface furnished partly by the vertebra with which the tubercle is connected, and partly by that next in front; so that the head of the first thoracic rib partly articulates with the centrum of the last cervical vertebra.

In all the Mammalia in which hind-limbs exist, that is to say, in all with the exception of the Sirenia and the Cetacea, there is a *sacrum* consisting of closely united vertebræ, the number of which varies in the different orders. The *caudal* region varies greatly as regards the degree of its development. In the caudal region of many Mammals there are developed a series of *chevron bones*—V-shaped bones, which are situated opposite the intervertebral spaces.

The centrum of each vertebra ossifies from three centres[1]—a middle one, an anterior, and a posterior. The middle centre forms the centrum proper; the anterior and posterior form the epiphyses. The epiphyses are less distinct in the Monotremes, and in the Dugong (*Sirenia*) have not been detected. Between successive centra are formed a series of discs of fibro-cartilage—the *inter-vertebral discs* — represented in lower Vertebrates only in Crocodiles and Birds. The anterior and posterior surfaces of the centra are nearly always flat.

The *sternum* consists of a number of segments—the *pre-sternum* in front, the *meso-sternum* or *corpus sterni*, composed of a number of segments or *sternebræ*, in the middle, and the *xiphi-sternum* behind. The sternum is in great part, though not completely,

[1] Usually the two centres of ossification which form the neural arches also contribute to the formation of the bony centrum.

formed in the fœtus by the separating off of the ventral ends of the ribs. Some of the Cetacea and the Sirenia are exceptional in having a sternum composed of a single piece of bone. The sternal ribs, by which the vertebral ribs are connected with the sternum, are usually cartilaginous, but frequently undergo calcification in

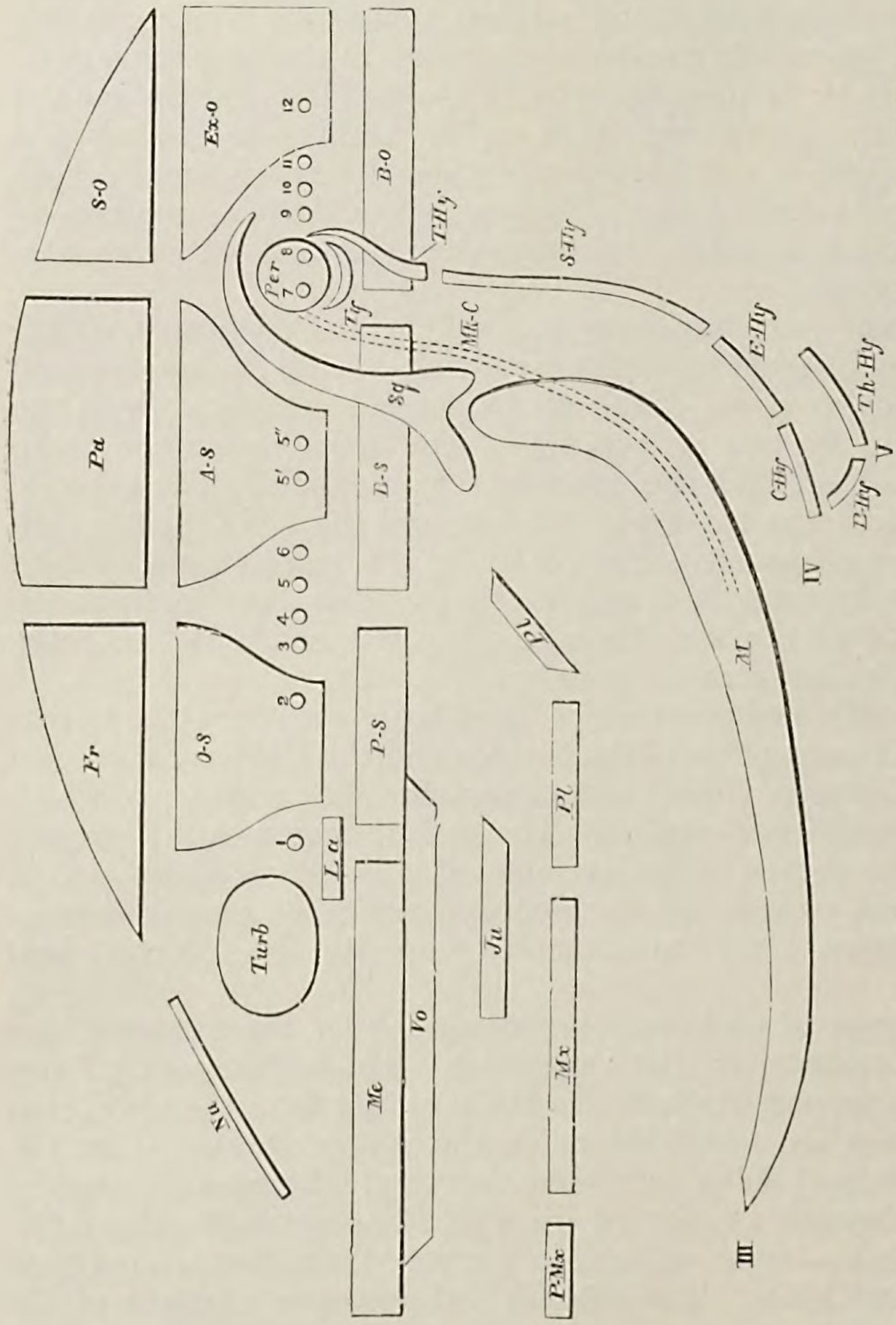


FIG. 1056.—Diagram of the relations of the principal bones of the Mammalian skull. **AS.** alisphenoid; **B-Hy.** basi-hyal; **B-O.** basi-occipital; **BS.** basisphenoid; **C-Hy.** cerato-hyal; **E-Hy.** epi-hyal; **ExO.** exoccipital; *Fr.* frontal; *Ju.* jugal; *La.* lacrymal; *M.* mandible; **ME.** mesethmoid; *Mx.* maxilla; *Na.* nasal; **OS.** orbitosphenoid; *Pa.* parietal; **Per.** periotic; *Pl.* palatine; **PS.** presphenoid; *P-Mx.* premaxilla; *Pt.* pterygoid; **S-Hy.** stylo-hyal; **S-O.** supra-occipital; *Sq.* squamosal; **T-Hy.** tympano-hyal; **Th-Hy.** thyro-hyal; **Turb.** turbinal; *Ty.* tympanic; *Vo.* vomer. The numbered circles indicate the points of exit of the cranial nerves: 1, olfactory; 2, optic; 3, oculo-motor; 4, trochlear; 5, 5′, 5″, the three divisions of the fifth nerve; 6, abducent; 7, facial; 8, auditory; 9, glossopharyngeal; 10; pneumogastric; 11, spinal accessory; 12, hypoglossal. (After Flower.)

old animals, and in some cases become early completely converted into bone.

The *skull* of a Mammal (Fig. 1056) contains the same elements and presents the same general regions as that of the Sauropsida, but exhibits certain special modifications. The bones of the skull,

with the exception of the auditory ossicles, the lower jaw, and the hyoid, are all immovably united together by means of sutures.

The *palatine bones* develop *palatine plates* separating off a posterior nasal passage from the cavity of the mouth, a condition found among the Sauropsida only in the Crocodilia, and, to a less extent, in the Chelonia and some Lizards.

The *zygomatic arch*, not found in the skull of the Sauropsida, being peculiar to Mammals, is a strong arch of bone formed partly of the squamosal, partly of the jugal and partly of the maxilla. The *orbit* in the skull of some Mammals is completely enclosed by bone, constituting a well-defined cavity; in others it is not completely surrounded by bone behind, and so communicates freely with the *temporal fossa*, which lies behind it.

The *periotic* bones (*pro-*, *opisth-* and *epi-otic*) become completely fused together in the skull of Mammals. Part of the periotic mass sometimes projects on the exterior at the hinder part of the lateral region of the skull, and is the *mastoid* portion; the rest is commonly called the *petrous* portion of the periotic, and encloses the parts of the internal ear—the mastoid portion containing only air-cells. The *tympanic* bone sometimes only forms a long tube, sometimes a mere ring of bone. In other cases it not only forms a tube for the external auditory meatus, but also forms the *bulla tympani*, a dilated bony process containing a cavity.

The *occipital* region presents two condyles for the articulation of the atlas.

The *mandible* consists in the adult of one bone on each side—the two rami, as they are called, being in most Mammals closely united at the symphysis. The mandible articulates with an articular surface, formed for it by the *squamosal* bone, below the posterior root of the zygomatic arch.

The *hyoid* consists of a body and two pairs of *cornua*—*anterior* and *posterior*; of these the anterior pair are longer, and consist of several bones, the most important and most constant of which is the *stylohyal*, connected usually with the periotic region of the skull. The posterior cornua or *thyro-hyals* are usually much smaller.

The ratio borne by the capacity of the cranial cavity to the extent of the facial region varies greatly in the different orders. The greater development of the cerebral hemispheres in the higher groups necessitates a greater development of the corresponding cerebral fossa of the cranium. This is brought about by the bulging upwards, forwards, and backwards of the cranial roof, resulting in a great modification in the primitive relations of certain of the great planes and axes of the skull (Fig. 1057). Taking as a fixed base line the *basi-cranial axis*, an imaginary median line running through the basi-occipital, basi-sphenoid, and presphenoid bones, we find that the great expansion of the cerebral fossa in the

higher Mammals leads to a great alteration in the relations to this axis (1) of the *occipital* plane or plane of the foramen magnum;

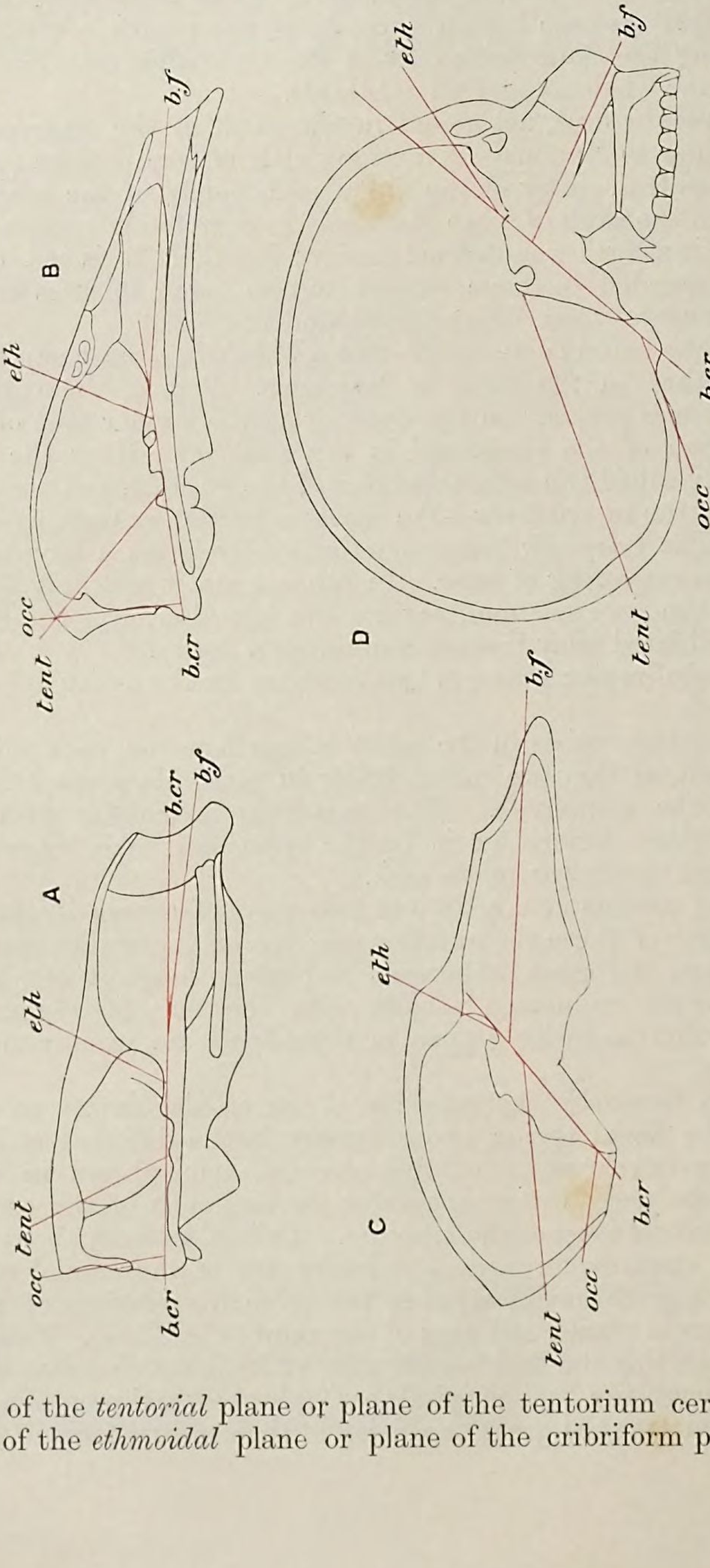


FIG. 1057.—Diagrams of sagittal sections of the skulls of various Mammals to show the modifications in the relations of the principal planes and axes. *A*, Koala (Phascolarctos); *B*, Dog; *C*, Baboon; *D*, Man. *b.cr.* basi-cranial axis; *b.f.* basi-facial axis; *eth.* ethmoidal plane; *occ.* occipital plane; *tent.* tentorial plane.

(2) of the *tentorial* plane or plane of the tentorium cerebelli; and (3) of the *ethmoidal* plane or plane of the cribriform plate of the

ethmoid. In the lower Mammals (*A*) these are nearly at right angles to the basi-cranial axis. In the higher groups, by the bulging forwards and backwards of the cranial roof, the occipital and tentorial planes incline backwards and the ethmoidal forwards, until all three may become approximately horizontal. At the same time, there is produced a change in the relations of the basi-cranial axis to the *basi-facial axis*—a line passing along the axis of the face between the mesethmoid and the vomer. In the lower forms the angle at which the basi-facial axis, when produced, meets the basi-cranial, is an exceedingly open one; in the higher forms, owing to the downward inclination of the facial region, this angle decreases in size, though it is never reduced to less than a right angle.

The *pectoral arch* of the Theria has fewer distinct elements than that of the Sauropsida. The coracoid, which in the latter is a large bone, taking a share at its dorsal end in the bounding of the glenoid cavity, and at its ventral end articulating with the sternum, is never present, in the adult, as a distinct bone. In the young of many Mammals it appears to be represented by a small ossification which enters into the glenoid facet; but this very soon coalesces with the scapula. The coracoid process, which is a separate ossification in the young Mammal, and, though in most instances completely fusing with the scapula, is sometimes recognisable as a distinct element up to a late period (many Marsupials, Sloths), appears to correspond to the bone called epicoracoid in the Prototheria (*vide infra*).

In the scapula a *spine* is nearly always developed, and usually ends in a freely-projecting acromion process. A *clavicle* is well developed in many Mammals, but is incomplete or absent in others. In the embryo there is, in the position of the clavicular bar, a bar of cartilage, which coalesces with its fellow in the middle line. The cartilaginous tract thus formed segments into five portions—a median, which coalesces with the pre-sternum, two small inner lateral, which unite with the clavicles, or are converted into the sterno-clavicular ligaments, and two long outer lateral, which give rise to the clavicles. The median and inner lateral portions appear to correspond to the epi-sternum of Reptiles and Prototheria. An additional small cartilage may represent the inner portion of the procoracoid of Amphibia. A piece of cartilage at the outer end of the clavicle proper is sometimes distinguishable —the *mesoscapular segment*.

In the carpus there are four proximal bones—*scaphoid, lunar, cuneiform*, and *pisiform*. The scaphoid corresponds to the radiale of the typical carpus (p. 76); the lunar perhaps represents a second centrale that occurs in some Amphibia; the cuneiform is probably the intermedium, and the pisiform the ulnare.

The *centrale* is present sometimes as a distinct ossification; the

five *distal carpals* are represented by the *trapezium*, *trapezoid*, *magnum*, and *unciform*, the last being the equivalent of the fourth and fifth distalia. There are never more than five digits, and in many forms the number is greatly reduced; only in certain Cetacea does the number of phalanges in a digit ever exceed three.

The three elements of the *pelvic arch* unite to form a single bone, the *innominatum*. The ilia unite by broad surfaces with the sacrum; the pubes unite in a *pubic symphysis*. All three usually take a share in the formation of the acetabulum, but the pubis may be shut out by a small *cotyloid bone*. In the shank the inner or *tibial* element is always the larger; the *fibula* may be rudimentary. A large sesamoid bone—the *patella*—is almost universally formed in close relation to the knee joint. In the tarsus there are two proximal bones, the *astragalus* and *calcaneum*, the latter undoubtedly corresponding to the fibulare of the carpus of lower Vertebrates, and the proximal part of the former to the intermedium and its distal portion to the proximal of the two central elements present in the tarsus of some Amphibia. The *scaphoid* or *navicular* represents the second central bone, and the distal row of tarsals are represented by the *cuboid* and the three *cuneiforms*.

The external form of the limbs and the mode of articulation of the bones vary in the various orders of the Mammalia, in accordance with the mode of locomotion. In most the habitual attitude is that which is termed the *quadrupedal*—the body being supported in a horizontal position by all four limbs. In quadrupedal Mammals the manus and pes sometimes rest on the ventral surfaces of the entire metacarpal and metatarsal regions as well as on the phalanges, when the limbs are said to be *plantigrade*, or on the ventral surfaces of the phalanges only (*digitigrade*) or on the hoofs developed on the terminal phalanges (*unguligrade*). Many of the quadrupeds have the extremities prehensile, the hand and foot being converted into a grasping organ. This is most marked in quadrupeds that pass the greater part of their life among the branches of trees, and in the Sloths the modification goes so far that both hands and feet are converted into mere hooks by means of which the animal is enabled to suspend itself body downwards from the branches of the trees.

Certain Mammals, again, have their limbs modified for locomotion through the air. The only truly *flying* Mammals are the Bats and the so-called Flying Foxes, in which the digits of the fore limb are greatly extended so as to support a wide delicate fold of skin constituting the wing. In other so-called flying Mammals, such as the Flying Squirrels and Flying Phalangers, there is no active flight, and the limbs undergo no special modification; the flying organ, if it may be so termed, in these cases being merely a

parachute or *patagium* in the form of lateral flaps of skin extending along the sides of the body between the fore and hind limbs.

Further, there are certain groups of *swimming* Mammals. Most Mammals, without any special modification of the limbs, are able to swim, and some of the quadrupeds, such as the Tapirs and Hippopotami, spend a great part of their life in the water. But there are certain Mammals in which the limbs are so specially modified to fit them for an aquatic existence—assuming the form of flippers or swimming paddles—that locomotion on land becomes almost, if not quite, impossible. Such are the Whales and Porpoises, the Dugongs and Manatees, and, in a less degree, the Seals and Walruses.

Skeleton cf Prototheria.—In the Prototheria (Fig. 1058) the epiphyses of the vertebræ are not well developed in the Platypus, and appear to be absent in Echidna. In both genera there is the normal number of vertebræ in the cervical region. The odontoid process long remains separate from the centrum of the axis. The cervical transverse processes are separately ossified, and only completely unite with the vertebræ at a late period, sutures being traceable in all but very old animals. Zygapophyses are absent in the cervical region. There are nineteen thoracico-lumbar vertebræ in both genera. The transverse processes are short, and the ribs do not articulate with them, but only with the sides of the centra. In the sacrum of Echidna there are three or four, in that of Platypus two, united vertebræ. The caudal region differs considerably in its development in the two genera. In Echidna the tail is very short, the vertebræ depressed, with no inferior spines, but with about five subvertebral bones, which differ from ordinary chevron bones in being mere flat nodules. In the Platypus the tail is very long, and the number of caudal vertebræ is twenty or twenty-one. Each has a distinct inferior spinous process (*infr. proc.*). The sternum consists of a pre-sternum and three keeled sternebræ: in Echidna but not in Platypus there is a xiphi-sternum. The most remarkable feature of the sternal apparatus in the Protheria is the presence of a T-shaped *epi-sternum* (interclavicle) (*epist.*) corresponding to that of Reptiles. The sternal ribs are ossified, and are connected with the vertebral ribs by imperfectly ossified intermediate ribs (*int. rbs.*).

The *skull* of the Monotremes differs widely from that of other Mammals. The bones early become fused together, so that it is difficult to trace their exact boundaries. The brain-case is larger and more rounded in Echidna than in Platypus, in accordance with the larger size of the brain in the former genus.

In Echidna (Fig. 1059) the squamosal extends further forwards than it usually does, and the posterior root of the zygomatic arch is further forward than in Mammals in general. The zygoma is

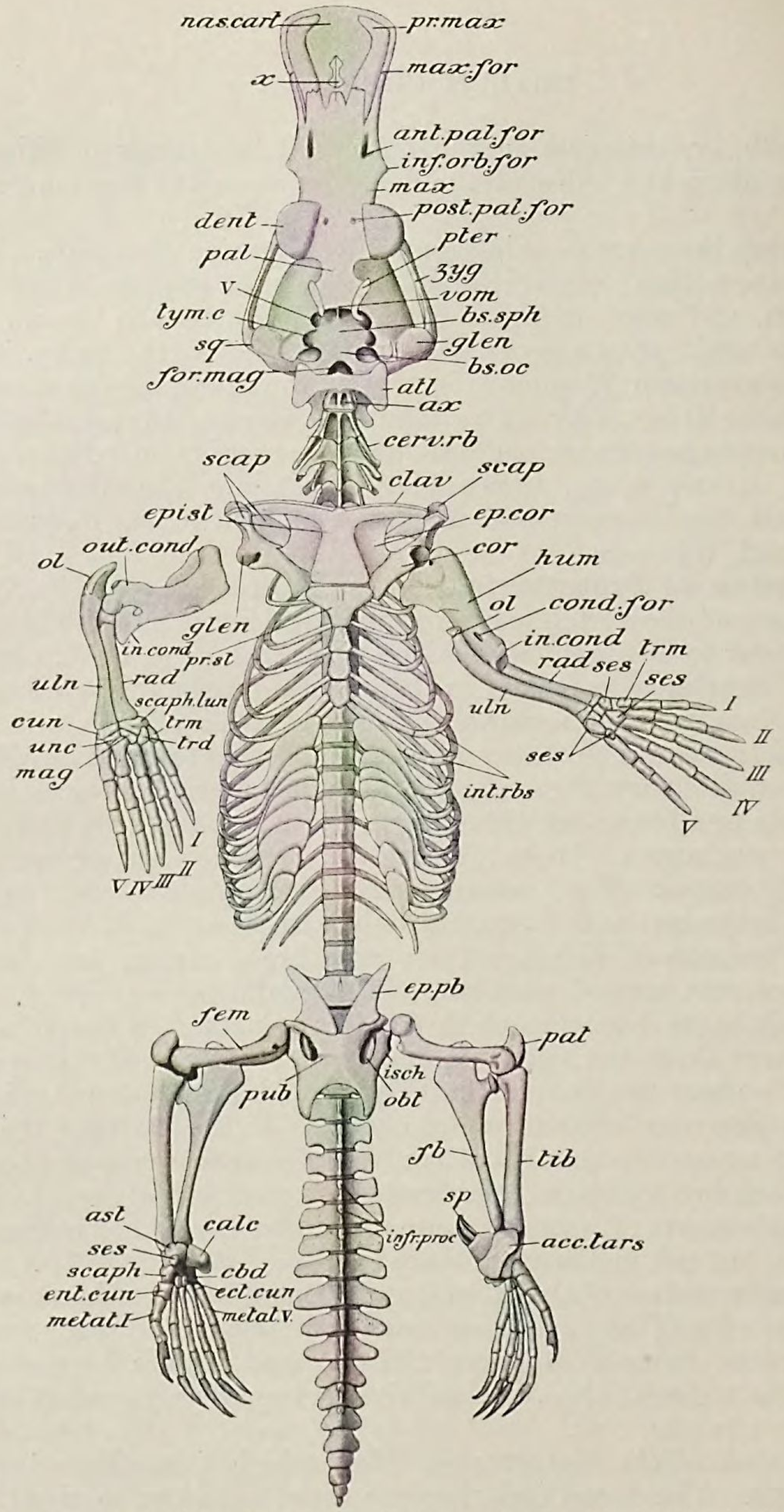


FIG. 1058.—Skeleton of male **Ornithorhynchus.** Ventral view. The right fore limb has been separated and turned round so as to bring into view the dorsal surface of the manus. The lower jaw is removed. *acc. tars.* accessory tarsal bone supporting the spur; *ant. pal. for.* anterior palatine foramen; *atl.* atlas; *ast.* astragalus; *ax.* axis; *bs.oc.* basi-occipital; *bs.sph.* basi-sphenoid; *calc.* calcaneum; *cbd.* cuboid; *cerv. rb.* cervical rib; *clav.* clavicle; *cond. for.* foramen above inner condyle of humerus; *cor.* coracoid; *cun.* cuneiform of carpus; *ect.cun.* ecto-cuneiform; *ent.cun.* ento-cuneiform; *ep.cor.* epicoracoid; *ep.pb.* epipubis; *fb.* fibula; *fem.* femur; *glen.* glenoid cavity of shoulder joint; *glen.* glenoid cavity for mandible; *hum.* humerus; *il.* ilium; *in. cond.* inner condyle of humerus; *inf. orb. for.* points to position of infra-orbital foramen; *infr. proc.* inferior processes of caudal vertebræ; *for. mag.* foramen magnum; *int. rbs.* intermediate ribs; *isch.* ischium; *mag.* magnum of carpus; *max.* maxilla; *max. for.* maxillary foramen; *metat. I*, first metatarsal; *metat. V*, fifth metatarsal; *post. pal. for.* posterior palatine foramen; *pr.max.* pre-maxilla; *pr.st.* pre-sternum; *pub.* pubis; *out. cond.* outer condyle of humerus; *rad.* radius; *scap.* scapula; *scaph.* scaphoid of tarsus; *scaph.lun.* scapho-lunar; *ses.* sesamoid bones of wrist; *sp.* tarsal horny spur; *tib.* tibia; *trd.* trapezoid; *trm.* trapezium; *troch. maj.* greater trochanter of femur; *troch. min.* lesser trochanter; *tym. c.* tympanic cavity; *uln.* ulna; *unc.* unciform; *vom.* vomer; *x*, dumb-bell shaped bone; *zyg.* zygomatic arch; *I—V*, digits of manus.

very narrow, and there is no rudiment of post-orbital processes. The alveolar border of the maxilla (*max.*) is narrow and devoid of teeth. The nasal and pre-maxillary region of the skull is drawn out into a long narrow rostrum. Near the anterior end of this is a rounded opening, the external nasal opening, which is entirely bounded by the pre-maxillæ—the nasals not extending so far

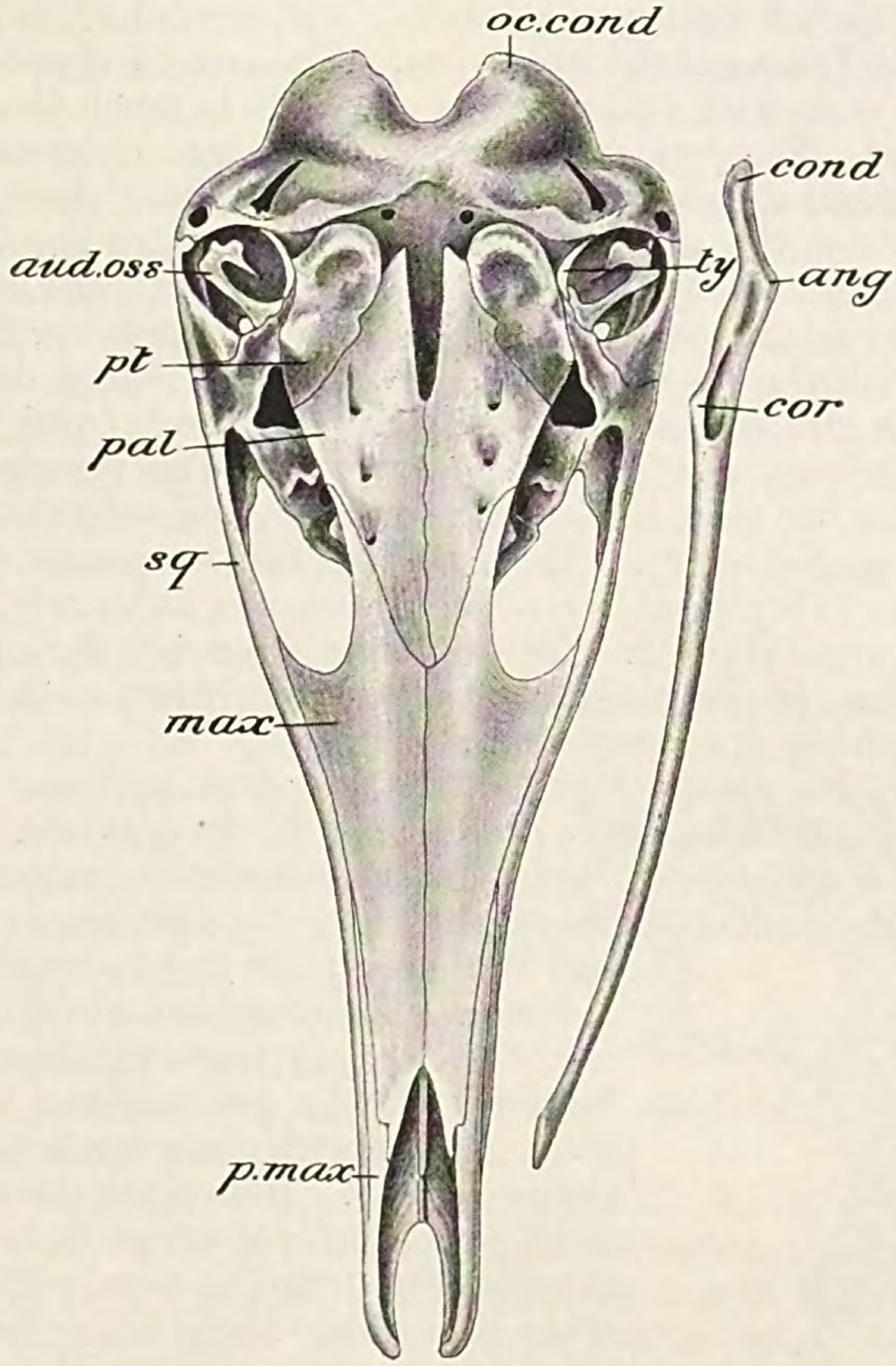


FIG. 1059.—**Echidna aculeata.** Ventral view of skull and right ramus of mandible. *ang.* angle of mandible; *aud. oss.* auditory ossicles; *cond.* condyle of mandible; *cor.* coronoid process; *max.* maxilla; *oc. cond.* occipital condyle; *pal.* palatine; *p. max.* pre-maxilla; *pt.* pterygoid; *sq.* squamosal; *ty.* tympanic ring.

forwards. An aperture in the nasal septum corresponds to an actual perforation by which the nasal cavities are in direct communication in the living animal. The pterygoids (*pt.*) are in the form of flat plates continuous with the bony palate; they extend back so as to form a part of the walls of the tympanic cavities. The tympanic (*ty.*) is an imperfect ring which does not become

united with the periotic. The mandible consists of very narrow, styliform rami, which are not firmly united at the symphysis. The condyle (*cond.*) is narrow, rather more elongated antero-posteriorly than transversely. There are very slight rudiments of the angle and of the coronoid process (*cor.*).

In the Platypus (Fig. 1058) the zygoma is stouter than in Echidna, and there is a rudimentary post-orbital process. The maxillary root of the zygoma develops a process which supports the horny teeth (*dent.*) of the upper jaw. The nasal and pre-maxillary region is expanded into a rostrum which is much broader than in Echidna. The premaxillæ (*pr. max.*) diverge from one another anteriorly, and then curve inwards again, partly enclosing a large space in which the nostrils are situated, and which is covered over in the recent state by the tough but sensitive hairless integument covering over the cartilage of the rostrum, the latter being continuous with the nasal septum. In this space between the premaxillæ is situated a dumb-bell shaped bone (*x*) which appears to be of the nature of an anterior vomer. The pterygoid (*pter.*) is much smaller than in Echidna, and does not extend as far back as the tympanic cavity. The mandible has its rami stouter than in Echidna; they meet for a short distance anteriorly, and then again diverge slightly. The condyle is much larger than in Echidna, and is elongated transversely. In front of it is a broad process bearing the horny tooth.

It is in the shoulder-girdle that we find perhaps the most striking peculiarities of the skeleton of the Prototheria. There is a T-shaped epi-sternum (*epist.*), as already stated, similar to that of Reptiles, the median limb articulating behind with the pre-sternum and the cross-piece closely applied to the clavicles. There are two short and broad coracoids (*cor.*) articulating internally and behind with the pre-sternum, and, externally, uniting with the scapula to form the glenoid cavity. In front of the coracoid is a flat plate, the epicoracoid (*ep. cor.*). The scapula (Fig. 1060) is very unlike that of other Mammals. There is a well-developed acromion process (*acr.*) with which the clavicle articulates; this terminates the anterior border, so that the latter would appear to correspond to the spine of the scapula of other Mammals. This is confirmed by the arrangement of the scapular muscles. The anterior part of the inner surface is in reality the pre-spinous fossa; the anterior portion of the outer surface the post-spinous fossa; and the part behind this, separated from it by a slight ridge,

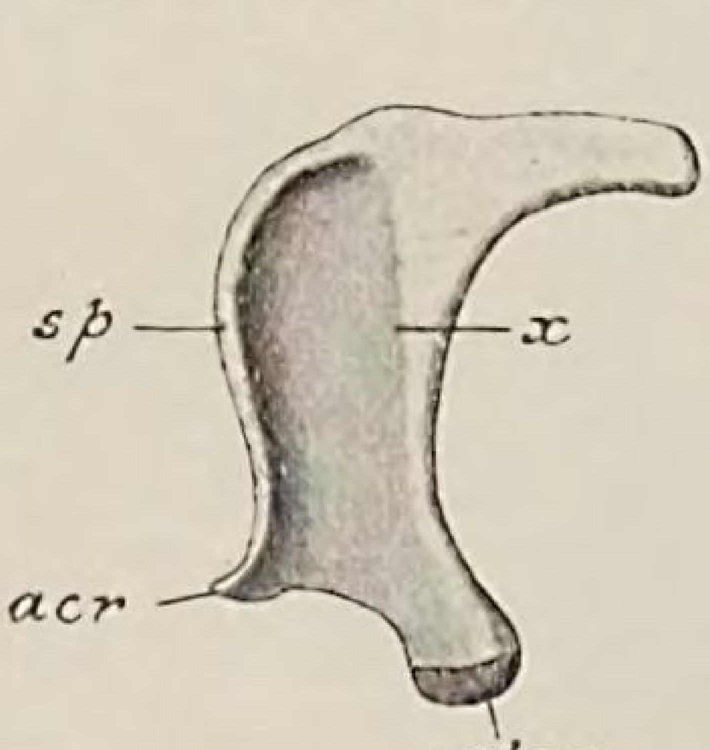


FIG. 1060.—Outer surface of left scapula of **Ornithorhynchus.** *acr.* process corresponding to acromion; *glen.* glenoid articular surface; *sp.* anterior border, corresponding to the spine; *x*, slight ridge which bounds the surface of origin of the sub-scapularis anteriorly.

together with the posterior portion of the inner surface, is the subscapular fossa.

The humerus is of remarkable shape, with greatly expanded extremities, especially in the Echidna, and prominent tuberosities and condyles. In the carpus the scaphoid and lunar are united; there is no separate centrale. There is a radial sesamoid, and two very large palmar sesamoids, which are sometimes united.

In the pelvis there is a very long symphysis in which pubes and ischia take an almost equal share. The acetabulum is perforated in both genera. With the anterior border of the pubes are articulated a pair of large epi-pubic or "marsupial" bones (Fig. 1059, *ep. pb.*). The femur has expanded extremities with prominent external and internal trochanters. There is a large ossified patella (*pat.*). The fibula (*fb.*) has at its proximal end a remarkable compressed process which ossifies from a separate centre, and greatly resembles the olecranon of the ulna. In the tarsus there are the usual bones. In the Platypus the astragalus and calcaneum are firmly united, and an accessory ossification (*acc. tars.*) on the inner side in the male bears the tarsal spur. The metatarsals are short and broad; as are the phalanges, except the last.

Skeleton of Metatheria.—In the Marsupials the inferior arch of the atlas (Fig. 1061) is often incompletely ossified, a gap being left in the prepared skeleton: sometimes the gap becomes closed in by the ingrowth of the lateral parts of the arch, sometimes a small separate ossification is developed filling up the opening. In the trunk there are always nineteen vertebræ. The transverse processes of the thoracic vertebræ are always well-developed, and the ribs articulate with them as well as with the bodies. Prominent metapophyses and anapophyses are developed; these are largest in the lumbar region. Only one sacral vertebra is present in most Marsupials; in some a second is ankylosed with it. The caudal region varies greatly in length. It is short in the Koala and the Wombat, long in the Opossums, Dasyures, Phalangers and Kangaroos (Fig. 1061). Chevron bones are generally present, except in the Koala and the Wombat.

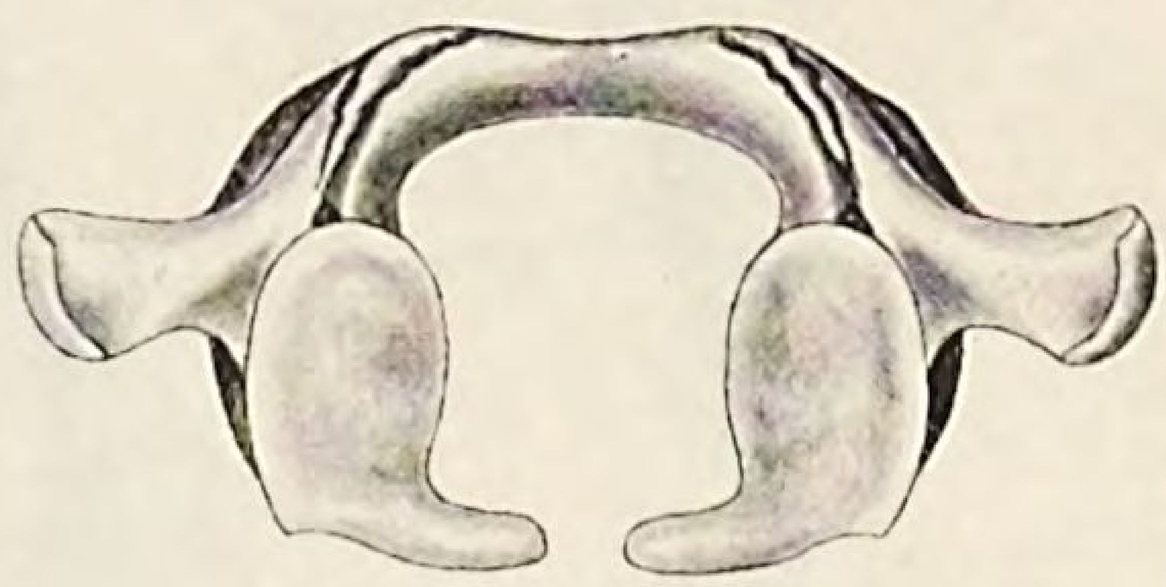


FIG. 1061.—Atlas of Kangaroo.

In the *skull* (Figs. 1063–1065) the brain cavity is relatively small, with the cerebellar fossa entirely behind the cerebral. The pituitary fossa is not distinct, and there are no clinoid processes. The zygoma is complete, but the orbit is not completely bounded by bone behind. The jugal extends beneath the squamosal

root of the zygoma to form part of the outer wall of the glenoid fossa. The lacrymal foramen is usually on the anterior margin of the orbit, sometimes on the face. The palate usually presents vacuities in its posterior portion. The pterygoid is always

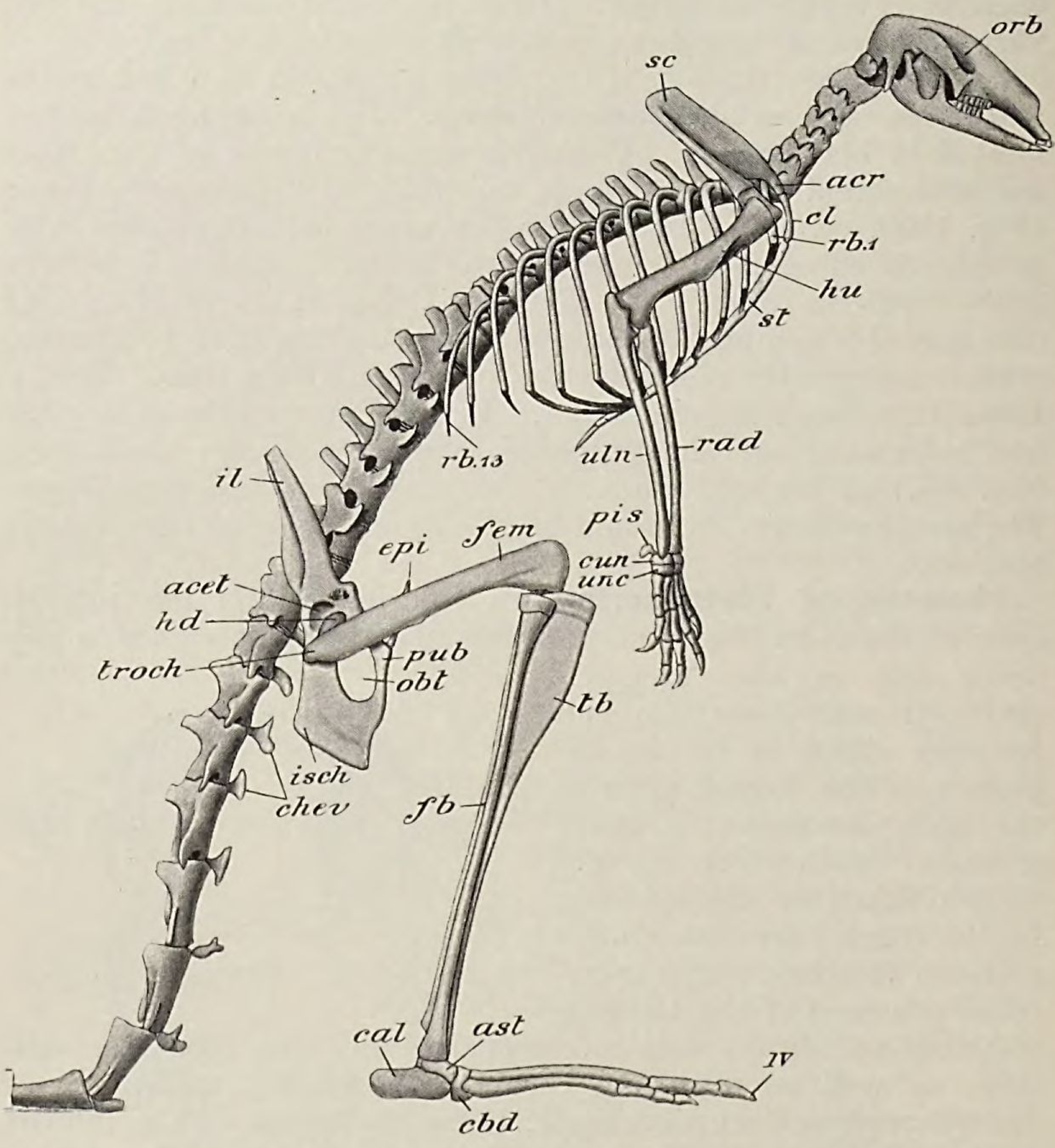


Fig. 1062.—Skeleton of **Wallaby** (*Halmaturus ualabatus*). The scapula is represented as raised somewhat higher than it would be in the natural relations of the parts. The head of the femur has been separated from the acetabulum. *acet.* acetabulum; *acr.* acromion process; *ast.* astragalus; *calc.* calcaneum; *cbd.* cuboid; *chev.* chevron bones; *cl.* clavicle; *cun.* cuniform of carpus; *epi.* epipubis; *fb.* fibula; *fem.* femur; *hd.* head of femur; *hu.* humerus; *il.* ilium; *isch.* ischium; *obt.* obturator foramen; *orb.* orbit; *pis.* pisiform; *pub.* pubis; *rad.* radius; rb^1. first rib; rb^{13}. last rib; *sc.* scapula; *st.* sternum; *tb.* tibia; *troch.* great trochanter of femur; *uln.* ulna; *unc.* unciform.

small. The alisphenoid is large, and forms the anterior boundary of the tympanic cavity; in the Kangaroos (Fig. 1064, *ali.*) it extends backwards so as to join the paroccipital process, which is greatly elongated. When an auditory bulla is developed, it is formed by

this bone, the tympanic being always small, and never ankylosed to neighbouring bones. The internal carotid artery perforates the

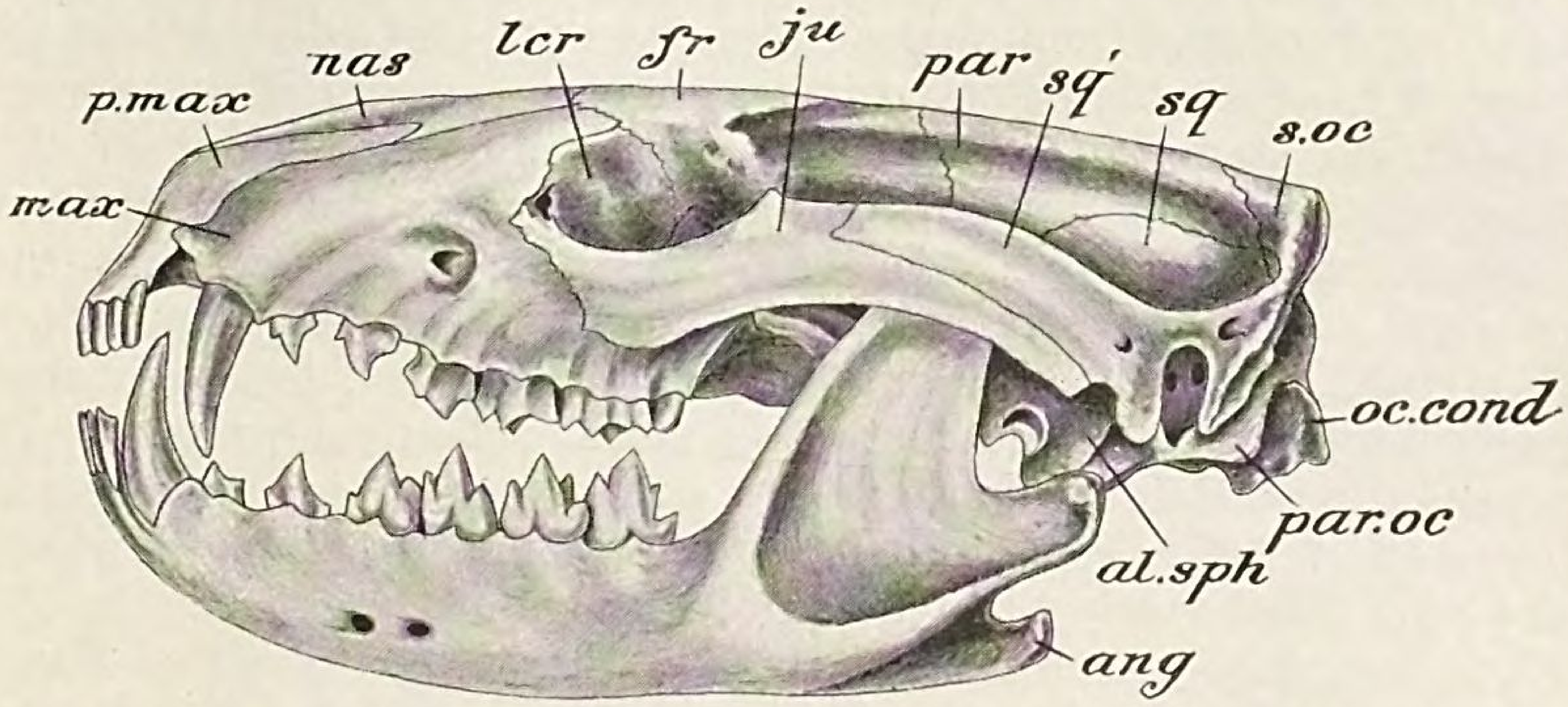


FIG. 1063.—Skull of **Dasyurus** (lateral view). *al.sph.* alisphenoid; *ang.* angular process of mandible; *fr.* frontal; *ju.* jugal; *lcr.* lacrymal; *max.* maxilla; *nas.* nasal; *oc. cond.* occipital condyle; *orb.sph.* orbitosphenoid; *par.* parietal; *par.oc.* paroccipital process; *p.max.* premaxilla; *s.oc.* supra-occipital; *sq.* squamosal; *sq'.* zygomatic process of squamosal.

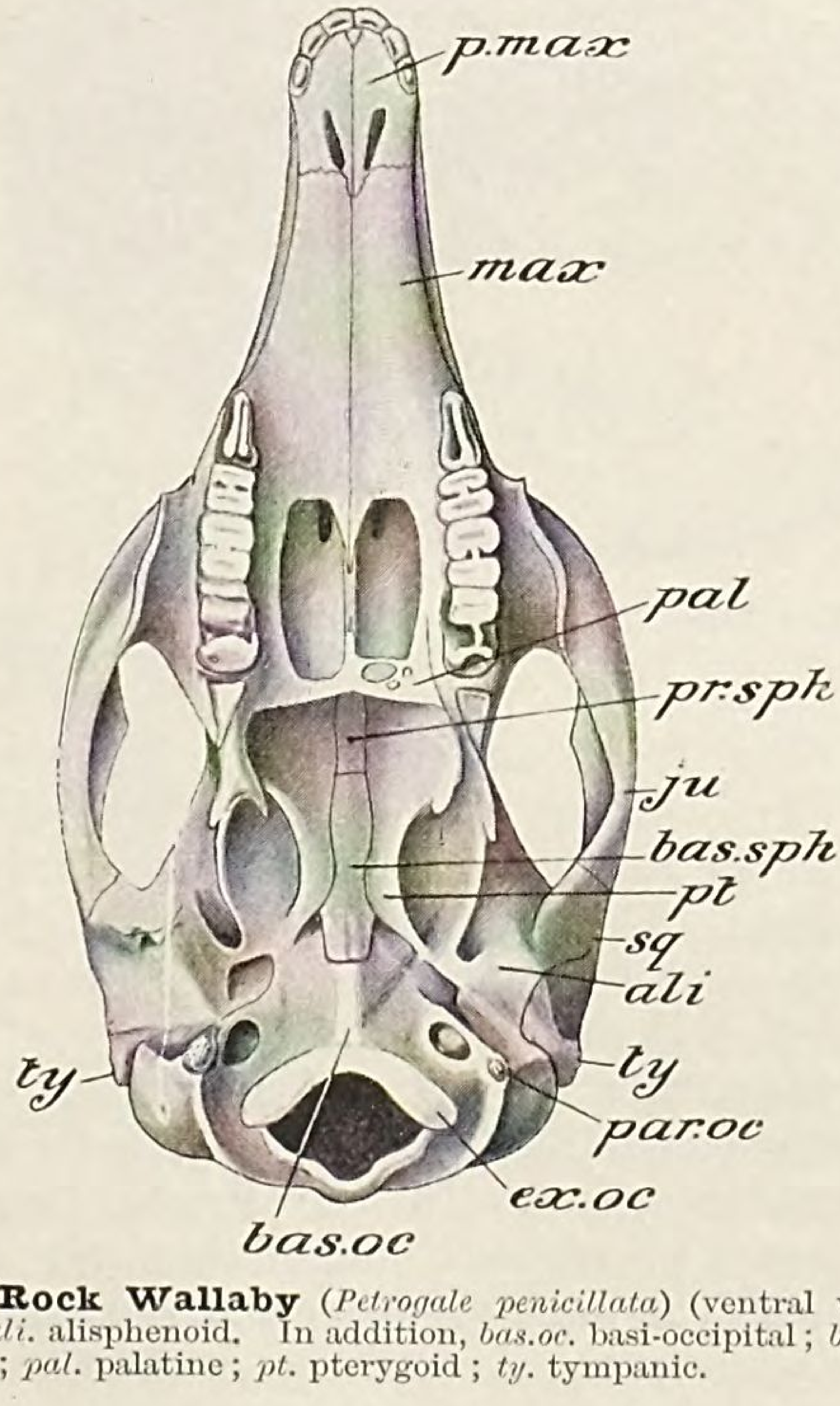


FIG. 1064.—Skull of **Rock Wallaby** (*Petrogale penicillata*) (ventral view). Letters as in Fig. 1063, except *ali.* alisphenoid. In addition, *bas.oc.* basi-occipital; *bas.sph.* basi-sphenoi ; *ex.oc.* ex-occipital; *pal.* palatine; *pt.* pterygoid; *ty.* tympanic.

basi-sphenoid. The optic foramen is not separate from the sphenoidal fissure. In all except *Tarsipes* the angle of the

mandible sends inwards a remarkable process (*ang.*), and is said to be *inflected*

In the *pectoral arch* of the Marsupials the coracoid process is, as usual, developed from a special bony centre, and a distinct suture is often recognisable between it and the scapula until a comparatively late stage. A clavicle is always present, except in the Bandicoots, but may be incomplete. There is never a distinct centrale in the carpus. In the Opossums the ilium has the primitive form of a straight, three-sided rod. In the Kangaroos (Fig. 1062, *il.*) it is still simple and three-sided, but somewhat curved outwards; in the rest it is more or less compressed. In nearly all the Marsupials there is a pair of epi-pubic or marsupial bones (Fig. 1062, *epi.*)—elongated and compressed bones which articulate posteriorly with the anterior edge of the pubes. In the Thylacine they are represented only by small unossified fibro-cartilages. In the leg the fibula is always well-developed. In

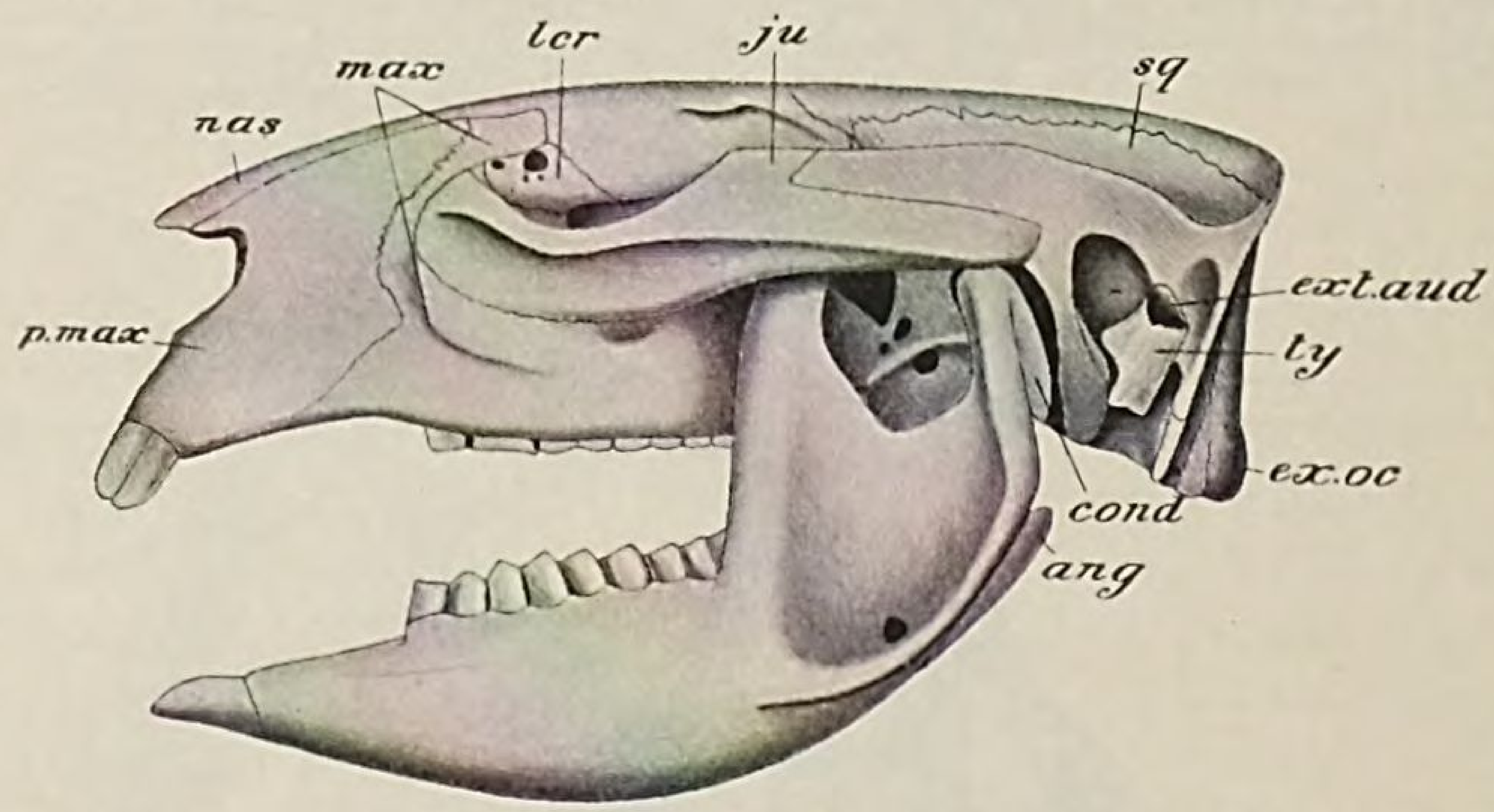


FIG. 1065.—Skull of **Wombat** (*Phascolomys wombat*) (lateral view). Letters as in Fig. 1063. In addition, *ext. aud.* opening of bony auditory meatus; *cond.* condyle of mandible.

the Phalangers (Fig. 1066) and the Koala there is always a considerable range of movement between it and the tibia, comparable in some degree to the movements of pronation and supination of the radius and ulna. The foot (Fig. 1067), as already stated in the account of the external characters, presents a much greater range of modification than the manus.

Skeleton of Edentata.—In the Armadillos more or fewer of the cervical vertebræ are ankylosed together both by their bodies and by their neural arches. In the lumbar region the metapophyses are greatly prolonged—longer than the transverse processes—and support the bony carapace. A remarkable peculiarity of the spinal column in the Armadillos is the fusion of a number of the anterior caudal vertebræ with the true sacrals to form the long sacrum, containing as many as ten vertebræ altogether (Fig. 1077). The caudal region is of moderate length; there are

numerous chevron bones. In *Manis*, *Orycteropus* and *Myrmecophaga* none of the neck vertebræ are united. In the posterior thoracic and the lumbar regions of *Myrmecophaga* there are developed complex accessory articulations between the vertebræ. The sacrum contains, in addition to the true sacral vertebræ, a number derived from the caudal region, a condition which occurs also in *Orycteropus*.

In the Sloths none of the cervical vertebræ are ankylosed together; but in the three-toed Sloths there is an important divergence from ordinary Mammals in the number of vertebræ in the cervical region, being nine instead of seven; while in one species of two-toed Sloth (*Cholœpus hoffmanni*) there are only six. The neural spines of all the vertebræ are very short. A number of the anterior caudal vertebræ are united firmly, though not quite fused, with one another and with the true sacrals.

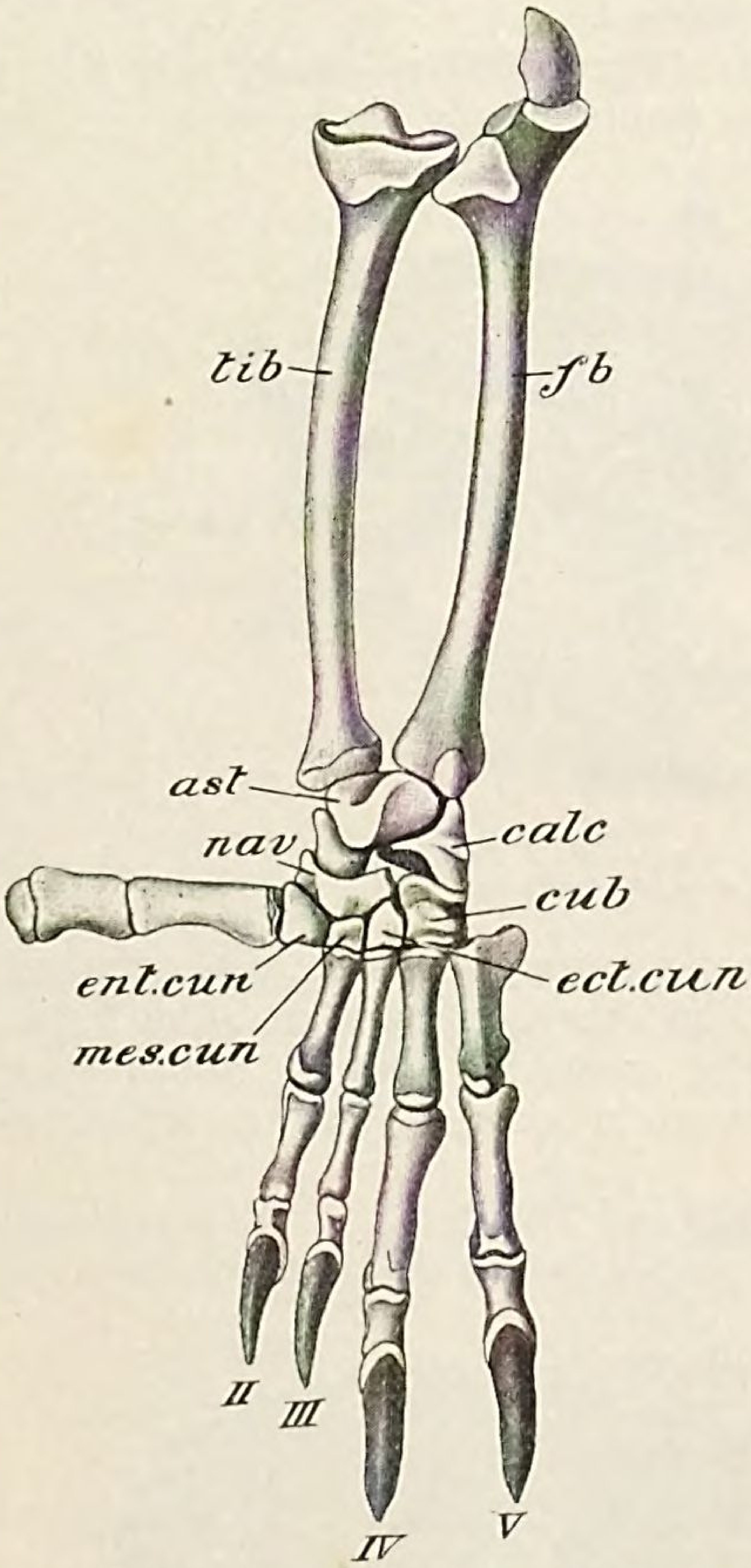


FIG. 1066.—Bones of leg and foot of **Phalanger.** *ast.* astragalus; *calc.* calcaneum; *cub.* cuboid; *ect. cun.* ecto-cuneiform; *ent.cun.* ento-cuneiform; *fb.* fibula; *mes. cun.* meso-cuneiform; *nav.* navicular; *tib.* tibia. (After Owen.)



FIG. 1067.—Bones of right foot of **Kangaroo** (*Macropus bennetii.*) *a.* astragalus; *c.* calcaneum; *cb.* cuboid; *c*3. ento-cuneiform; *n.* navicular. (After Flower.)

In the Armadillos the sternal ribs, which are sub-bifid at their sternal ends, are ossified, and articulate with the sternum by means

of well-developed synovial articulations. In the American Anteaters there are similar synovial joints, and the sternal ends of the sternal ribs are completely bifid. In the Sloths the sternum is long and narrow, and there are no synovial joints. In front the sternal ribs are ossified and completely united with the vertebral ribs, but behind they are separated from the latter by intermediate ribs which are less perfectly ossified.

In the Armadillos the *skull* (Fig. 1068) is broad and flat, the facial region triangular. The tympanic (*ty.*) is in some developed

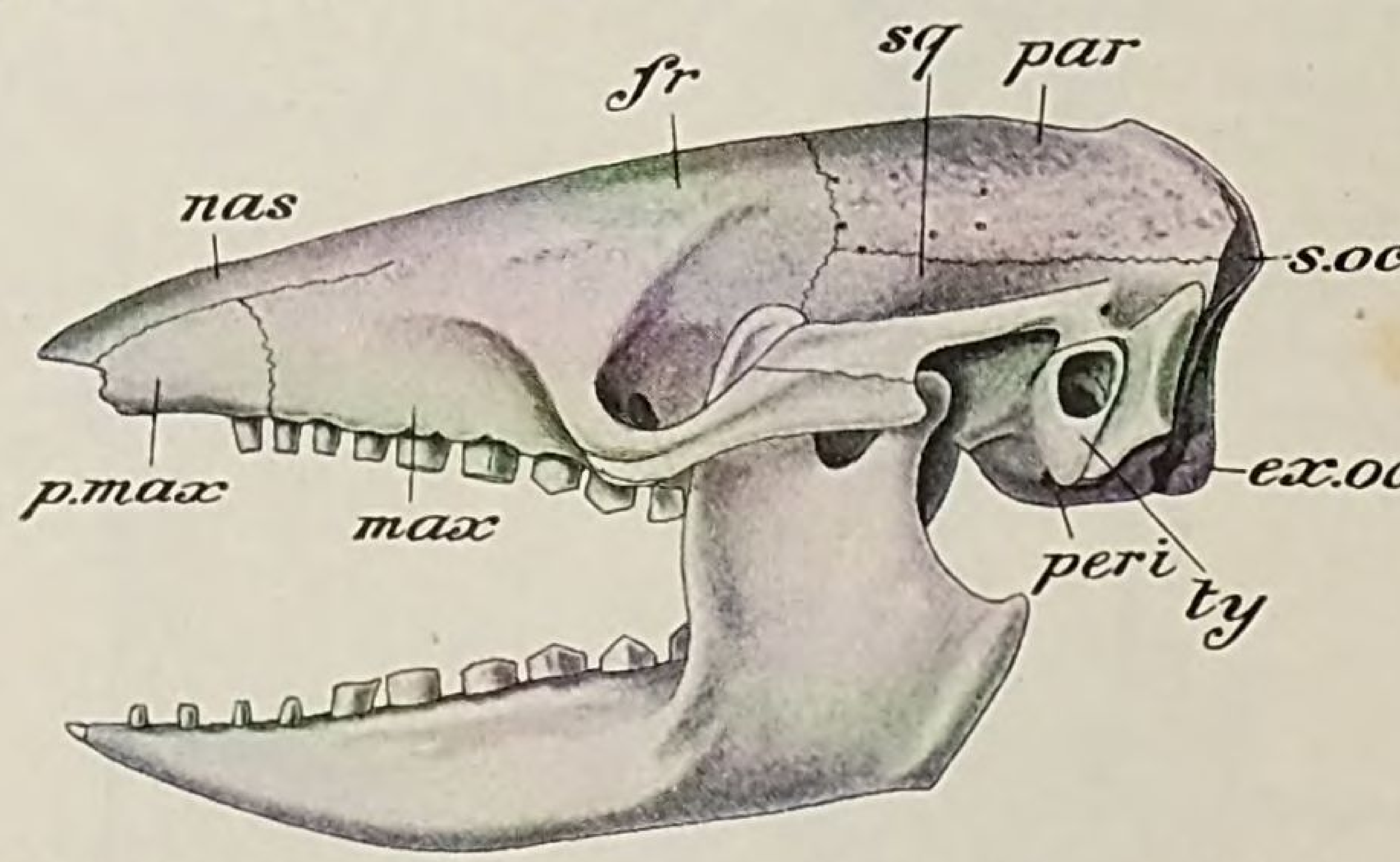


FIG. 1068.—Skull of **Armadillo** (*Dasypus sexcinctus*). Letters as in Fig. 1063. In addition *peri.* periotic; *ty.* tympanic.

into a bulla. The bony auditory meatus is in some cases elongated. The zygoma is complete. The pterygoids are small, and do not develop palatine plates. The mandible has a well-developed ramus with a prominent coronoid process and a well-marked angular process.

In the Anteaters (Figs. 1069 and 1070) the skull is extremely long and narrow—the facial region being drawn out into a long

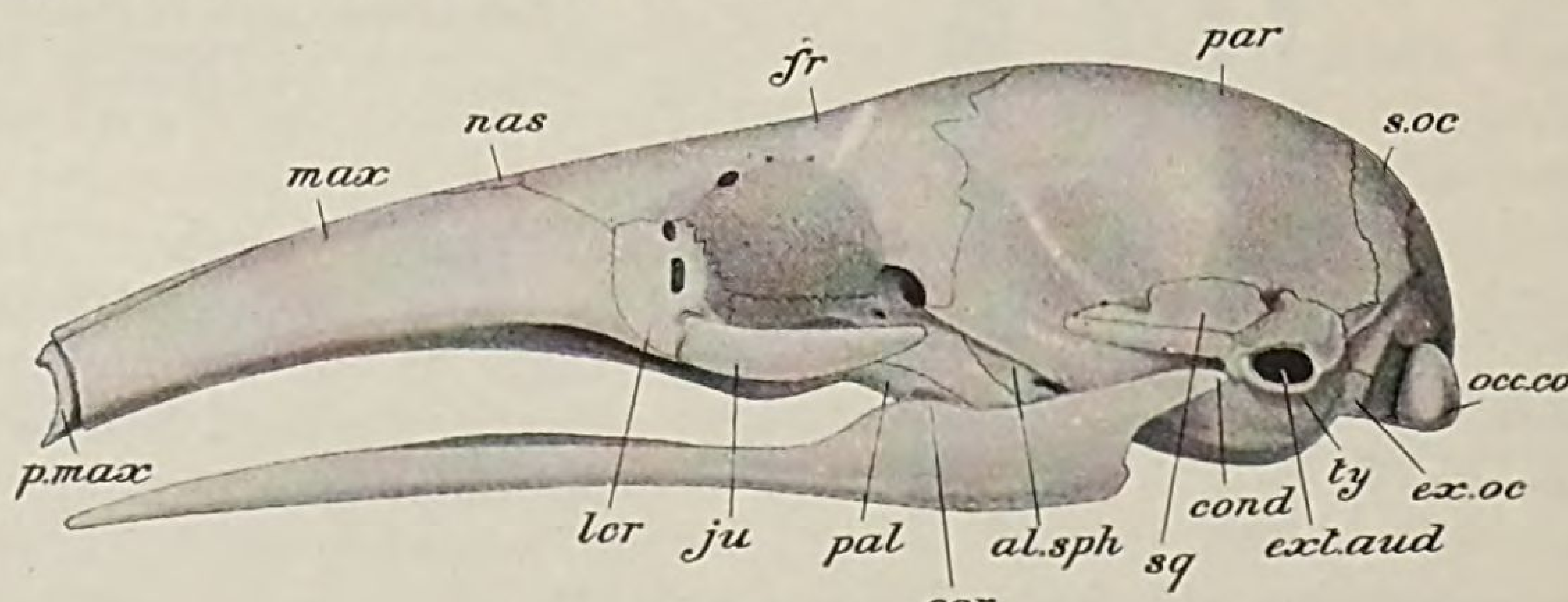


FIG. 1069.—Skull of **Anteater** (*Myrmecophaga*), lateral view. *al.sph.* alisphenoid; *cond.* condyle of mandible; *cor.* coronoid process of mandible; *ex. oc.* ex-occipital; *ext. aud.* external auditory meatus; *fr.* frontal; *ju.* jugal; *lcr.* lacrymal; *max.* maxilla; *nas.* nasal; *occ. cond.* occipital condyle; *pal.* palatine; *par.* parietal; *p.max.* pre-maxilla; *s.oc.* supra-occipital; *sq.* squamosal; *ty.* tympanic.

narrow rostrum, with the external nares at its extremity. The olfactory fossæ are greatly developed. The rostrum is composed

of mesethmoid, vomer, maxillæ and nasals—the premaxillæ being very small. The zygoma is incomplete, and the orbit is not closed behind by bone: the post-orbital processes of the frontal being entirely absent. The pterygoids (*pter.*) in all but Cycloturus, develop palatine plates. There is no bony auditory meatus. The mandible is entirely devoid of ascending ramus—consisting of two long and slender horizontal rami, with a very short symphysis.

In the Sloths (Fig. 1071) the cranial region is elevated and rounded, the facial short; the frontal region is elevated, owing to the development of extensive frontal air-sinuses. The premaxillæ are small, and not firmly connected with the maxillæ, so that they are commonly lost in the macerated skull. The jugal (*ju.*) develops a strong zygomatic process which bifurcates behind into two branches, neither of which is connected with the rudimentary zygomatic process of the squamosal, so that the

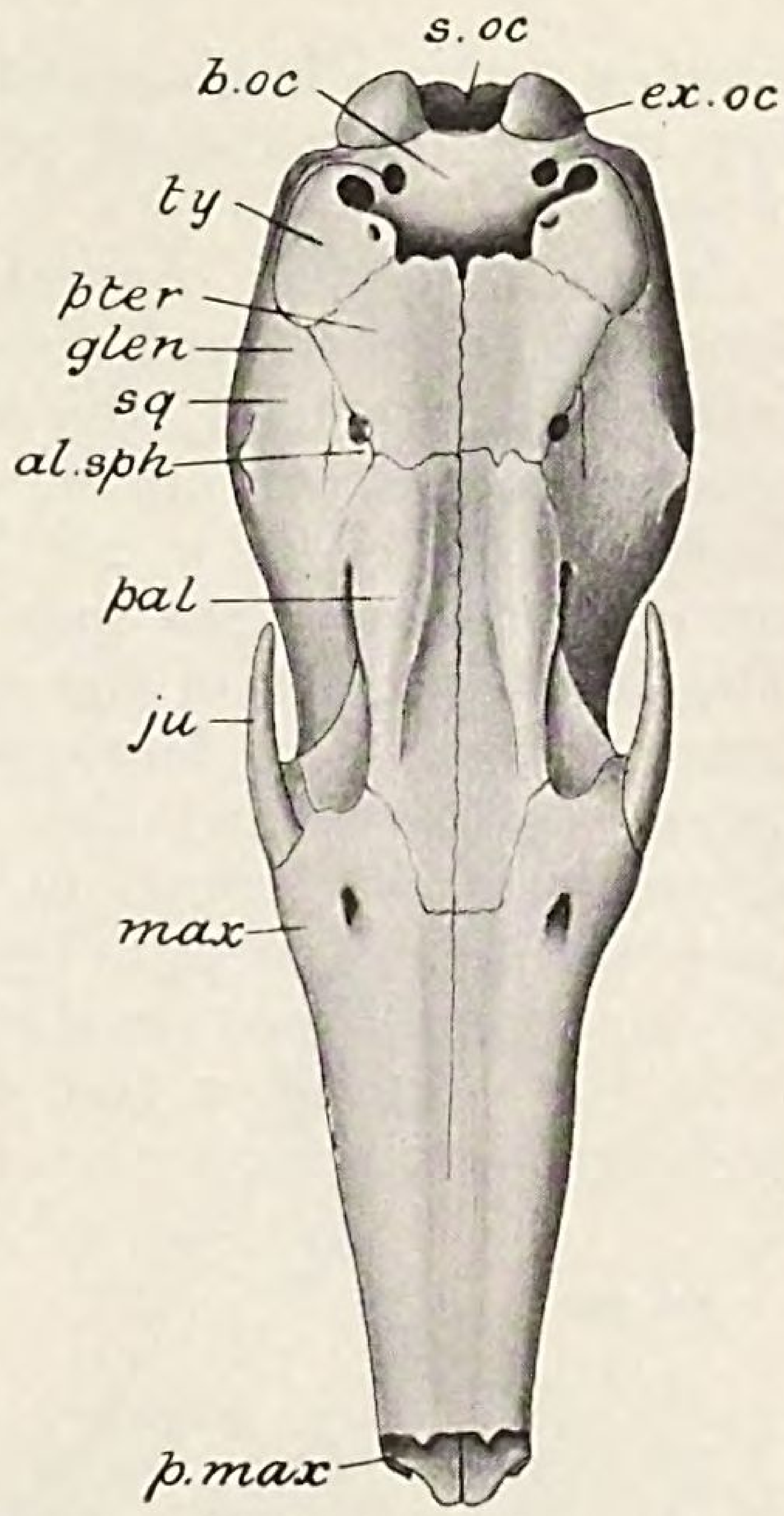


FIG. 1070.—Skull of **Anteater** (*Myrmecophaga*), ventral view. Letters as in Fig. 1069. In addition, *b.oc.* basi-occipital; *glen.* glenoid surface for mandible; *pter.* pterygoid.

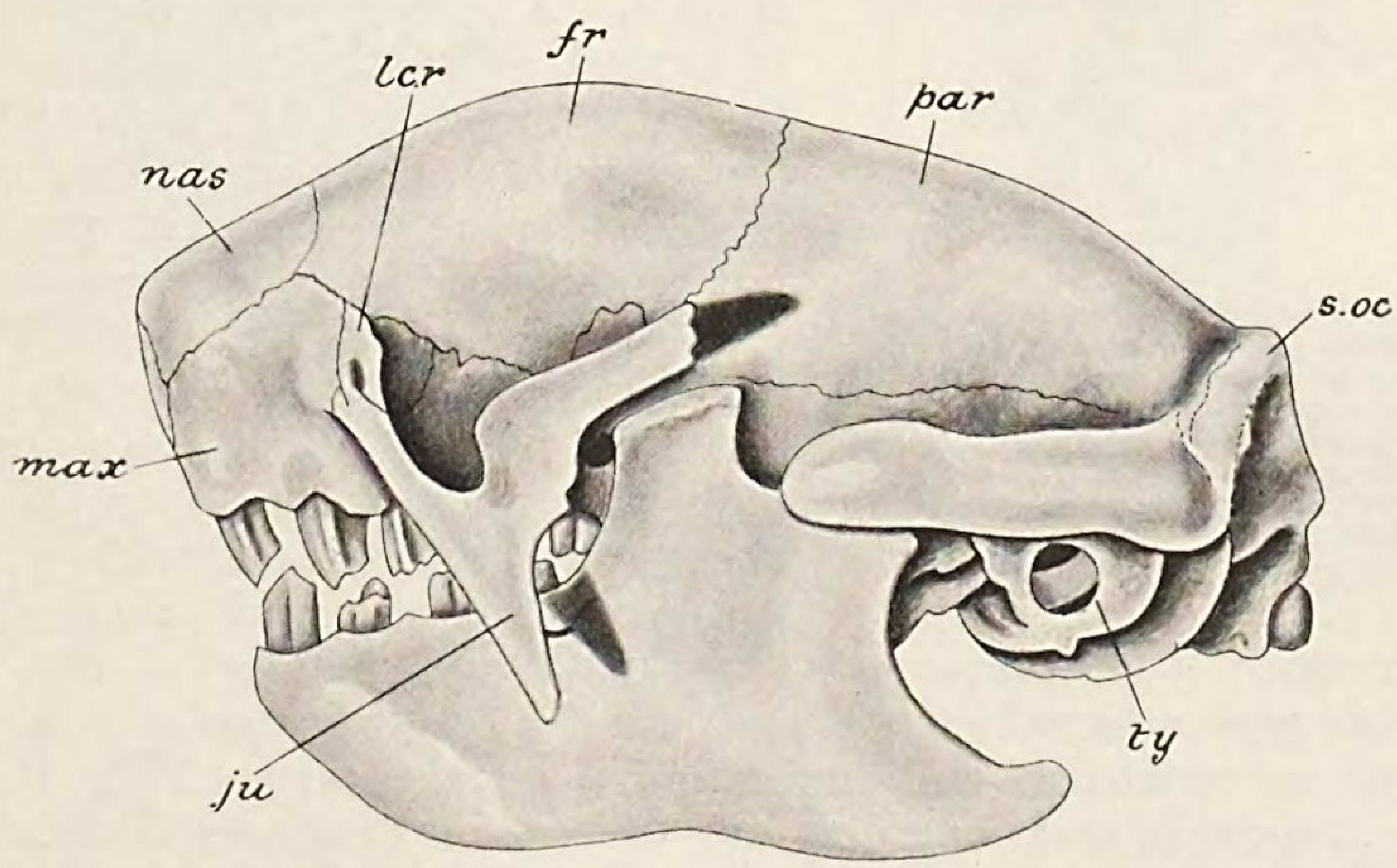


FIG. 1071.—Skull of **Three-toed Sloth** (*Bradypus tridactylus*). Letters as in Fig. 1069.

zygomatic arch remains incomplete. There are, at most, the rudiments of post-orbital processes of the frontals. The pterygoids

develop vertical laminæ and form no palatine plates. The ascending ramus and coronoid process of the mandible are both well developed.

In the American Anteaters and Armadillos, the bones of the *fore-limb* are short and powerful. The scapula in the Anteaters is broad and rounded; the anterior border unites with the coracoid process so as to convert the coraco-scapular notch into a foramen. In the middle of the spine there is a triangular process: a ridge on the infra-spinous fossa presents the appearance of a second spine. The fibres of origin of the subscapularis muscle extend on to the outer surface as far forward as this ridge, so that the part of the outer surface behind the ridge corresponds to a part of the subscapular fossa, which in other Theria is co-extensive with the inner surface. Except in *Cycloturus* the clavicles are rudimentary. All the carpal bones are distinct.

In the Armadillos the scapula (Fig. 1072) has an extremely prolonged acromion (*acr.*), sometimes articulating with the humerus The ridge (*sp′.*) representing a second spine is present. The clavicle is well developed. The humerus is short and powerful with well developed processes and ridges, and with a foramen above the inner condyle (*entepicondylar foramen*). The carpus consists of the ordinary eight bones.

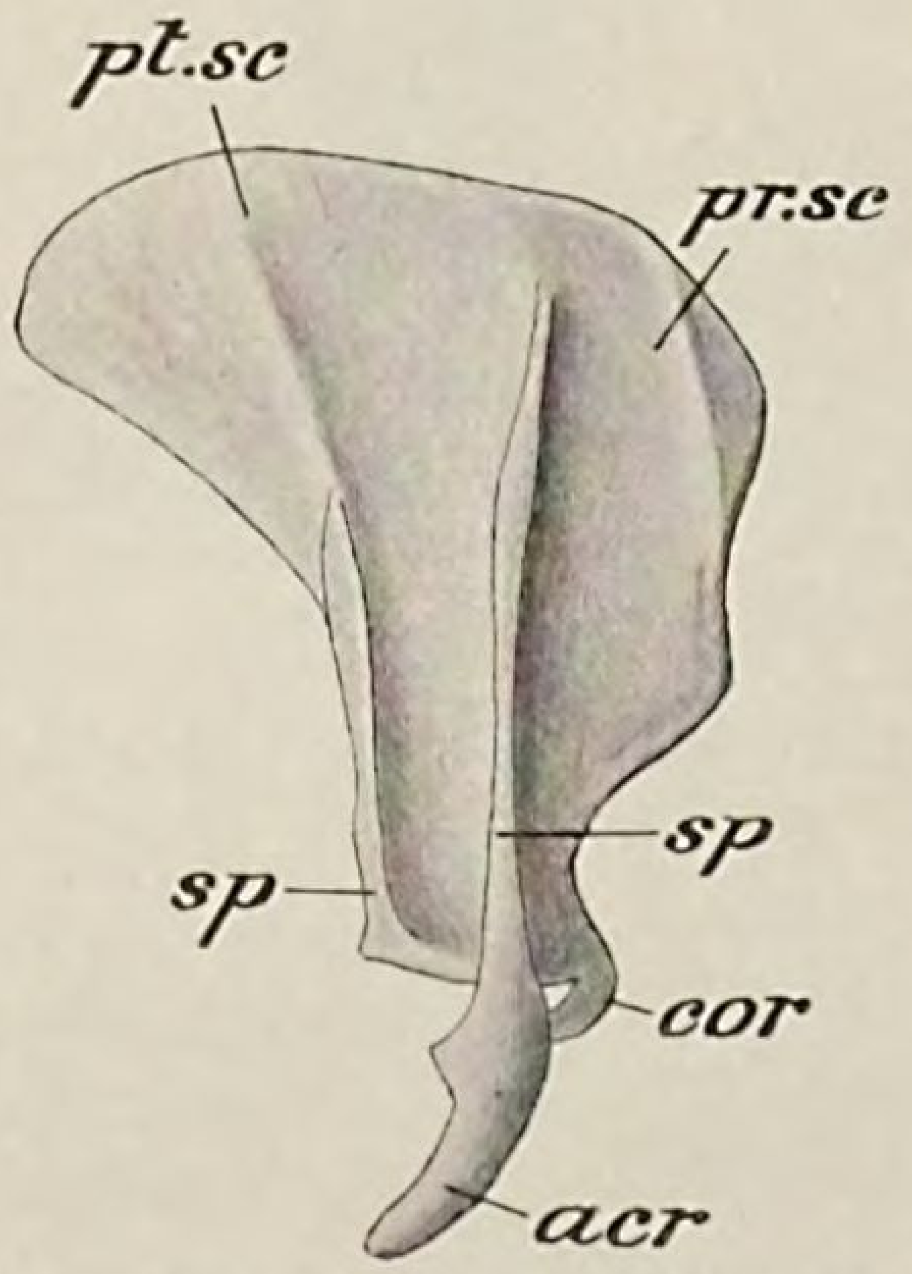


FIG. 1072.—Shoulder-girdle of **Armadillo** (*Dasypus sexcinctus*). *acr.* acromion; *cor.* coracoid process; *pr. sc.* pre-spinous fossa; *pt.sc.* post spinous fossa; *sp.* spine; *sp′.* ridge probably marking the anterior limit of origin of the subscapularis muscle.

In the Sloths (Fig. 1073) the bones are comparatively long and slender. A coraco-scapular foramen is formed as in the Anteaters. In the three-toed Sloths (Fig. 1074) the acromion (*acr.*) is at first connected with the coracoid process, but becomes reduced and loses the connection; in the two-toed Sloth the connection persists. The clavicle (*cl.*) is not directly connected internally with the sternum; externally it is connected with the coracoid process —a condition observed in no other Mammal. The humerus is very long and slender, so are the radius and ulna, which are capable of a certain amount of movement in pronation and supination. In the carpus (Fig. 1075) the trapezoid and magnum are united in *Bradypus*, distinct in *Cholœpus*: in the former the trapezium is usually fused with the rudimentary first metacarpal. The first and fifth metacarpals are represented only by rudiments. The proximal phalanges of the three digits are early ankylosed with the corresponding meta-

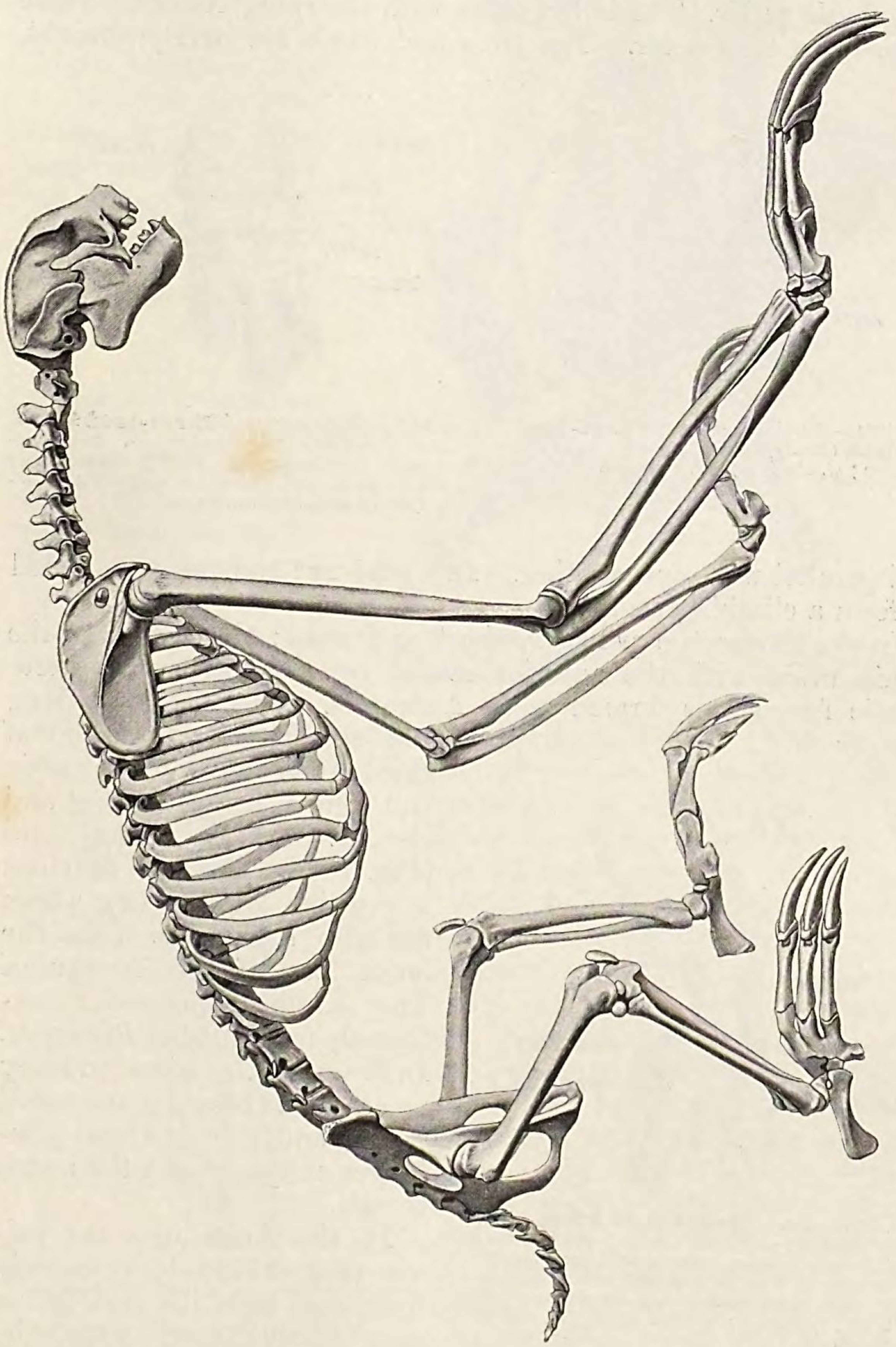


FIG. 1073.—Skeleton of **Three-toed Sloth** (*Bradypus tridactylus*). After Blainville.

carpals, so that it might readily be supposed that one of the ordinary bones of the digit was absent.

The *pelvis* of the American Anteaters is elongated, with a short symphysis pubis. The ischia unite with the spinal column. There is no third trochanter. The tibia and fibula are nearly straight,

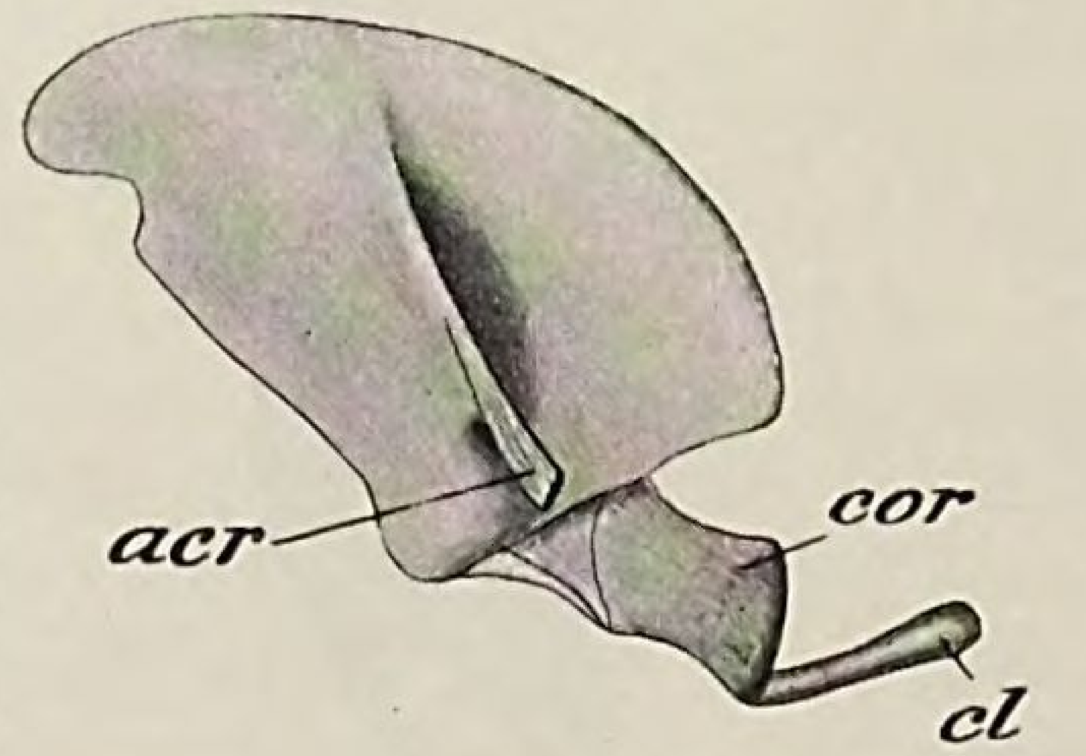


FIG. 1074.—Shoulder-girdle of **Three-toed Sloth** (*Bradypus tridactylus*). *acr.* acromion; *cl.* clavicle; *cor.* coracoid.

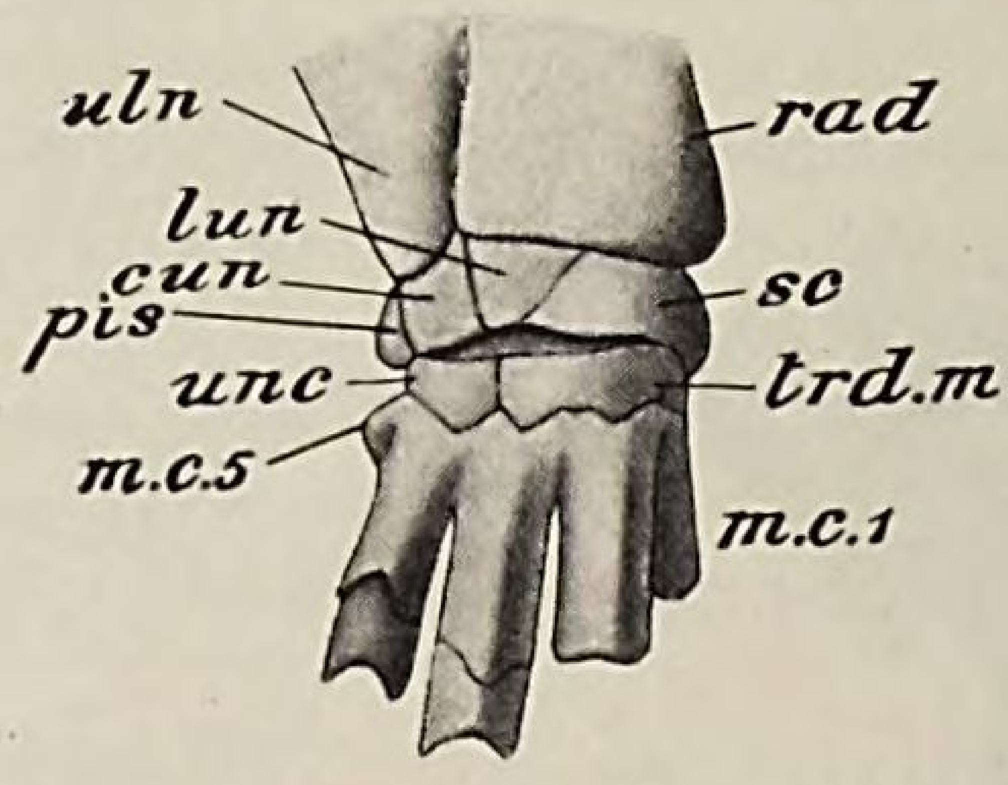


FIG. 1075.—Right manus of **Three-toed Sloth** *cun.* cuneiform; *lun.* lunar; *mc*[1]. first metacarpal; *mc*[5]. rudiment of fifth metacarpal; *pis.* pisiform; *rad.* radius; *sc.* scaphoid; *trd. m.* trapezoid and magnum united

and parallel with one another. In *Cycloturus* the pes is modified to form a climbing organ.

In the Sloths the pelvis is short and wide; the spines of the ischia unite with the anterior caudal vertebræ so that a sacrosciatic foramen is formed as in Anteaters. The femur is long and slender; it is devoid of third trochanter. The tibia and fibula are also long and slender. At its distal end (Fig. 1076) the fibula develops a peg-like process (x) which fits into a depression in the outer face of the astragalus. The calcaneal process is extremely prolonged in *Bradypus*. In *Bradypus* there is a tendency to ankylosis between the tarsal bones, and the proximal phalanges ankylose with the metatarsals.

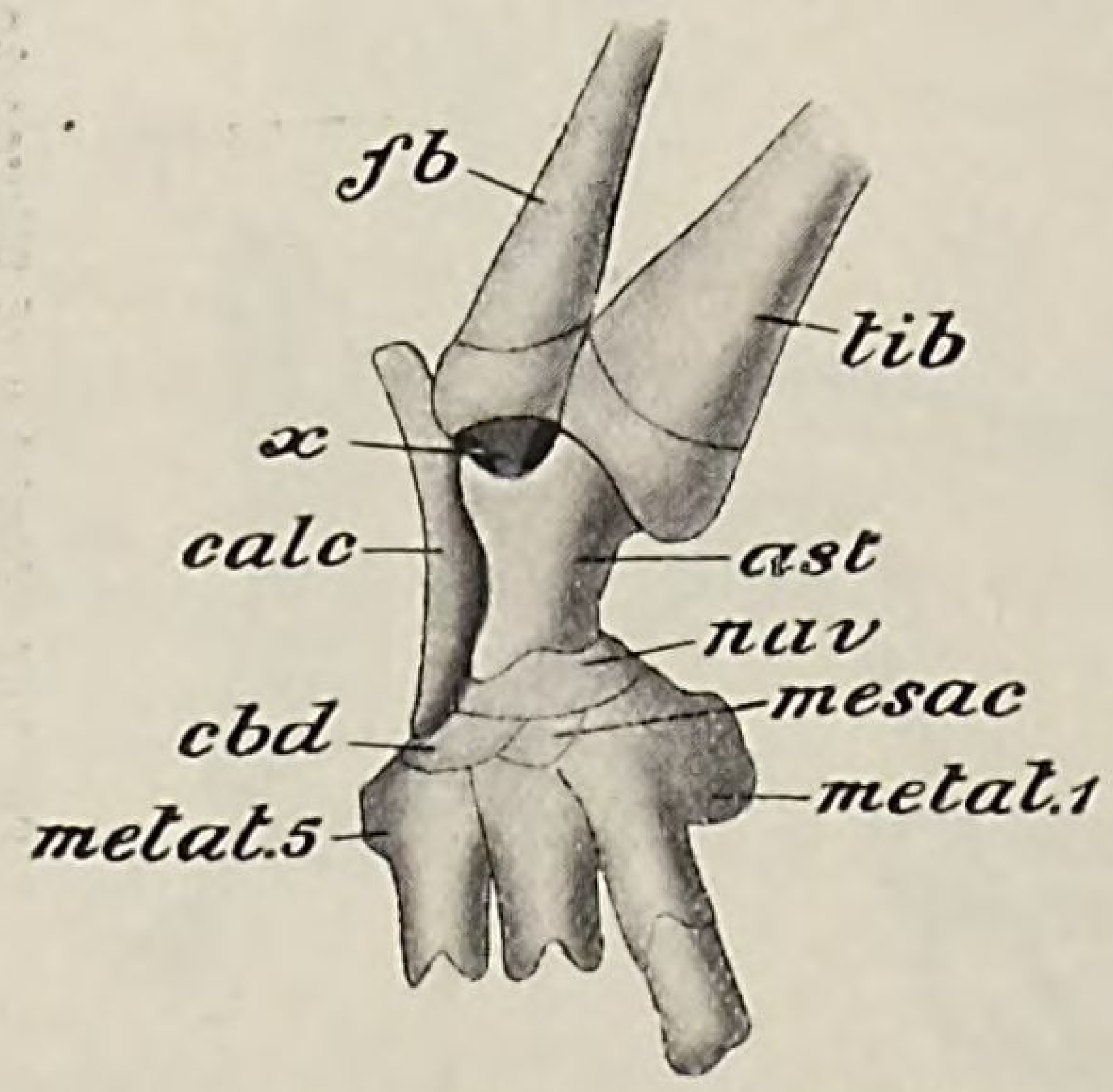


FIG. 1076.—Pes of **Three-toed Sloth.** *ast.* astragalus; *calc.* calcaneum; *cbd.* cuboid; *fb.* fibula; *mesoc.* mesocuneiform; *metat*[1]. vestige of first metatarsal; *metat*[5]. vestige of fifth metatarsal; *nav.* navicular; *tib.* tibia; *x*, peg-like process at distal end of fibula.

In the Armadillos the pelvis (Fig. 1077) is extremely long, and both ilia and ischia are firmly fused with the spinal column. The femur has a prominent third trochanter. The bones of the pes (Fig. 1078) are normal.

Skeleton of Cetacea.—In the Cetacea (Fig. 1079) the cervical region (*cerv.*) is always very short, and the constituent vertebræ are often completely fused together into a continuous bony mass, or the atlas alone may be separated from the rest; but sometimes all the vertebræ are complete and separate. In the latter case they have small arches and long transverse processes consisting of two narrow bars with a wide space between them. The epiphyses are very distinct discs which often remain separate from the bodies up to a late period. The neural spines are well developed. The zygapophyses are not well developed, and are absent in the posterior portion. In the absence of hind limbs there is no sacral region. The caudal region consists of numerous vertebræ beneath which, opposite the intervertebral spaces, are a series of chevron bones (*chev.*).

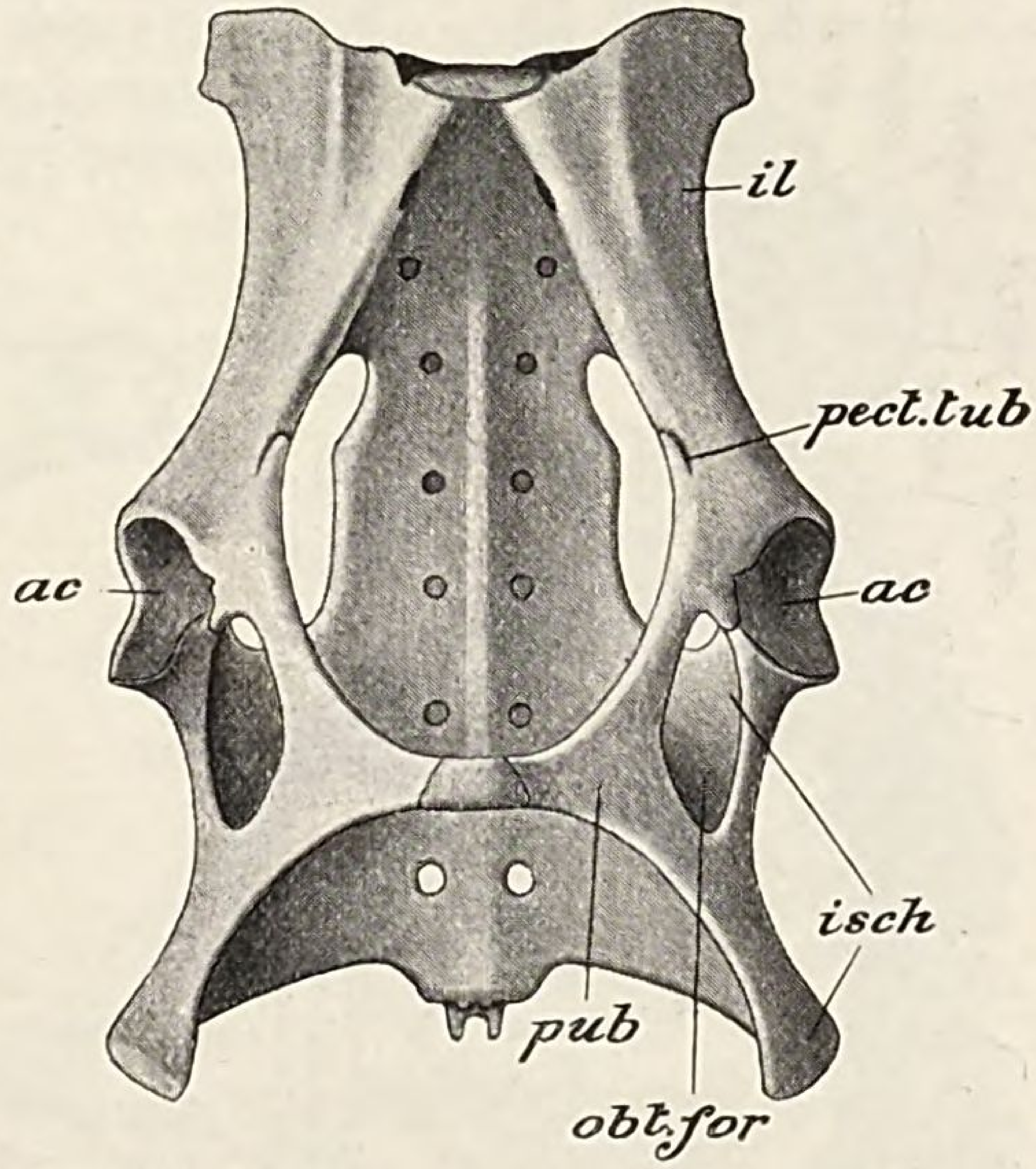


Fig. 1077.—Pelvis and sacrum of **Armadillo** (*Dasypus sexcinctus*). *ac.* acetabulum; *il.* ilium; *isch.* ischium; *obt. for.* obturator foramen; *pect. tub.* pectineal tubercle; *pub.* pubis.

In the Whale-bone Whales only one pair of ribs articulates with the sternum, and none articulate with the bodies of the vertebræ, but only with the transverse processes. In the Toothed Whales only a small number are connected with the sternum, sometimes through the intervention of intermediate ribs, and the anterior few only, in most cases, articulate with the bodies of the vertebræ; but in some a greater number articulate with both transverse processes and bodies by distinct tubercles and heads.

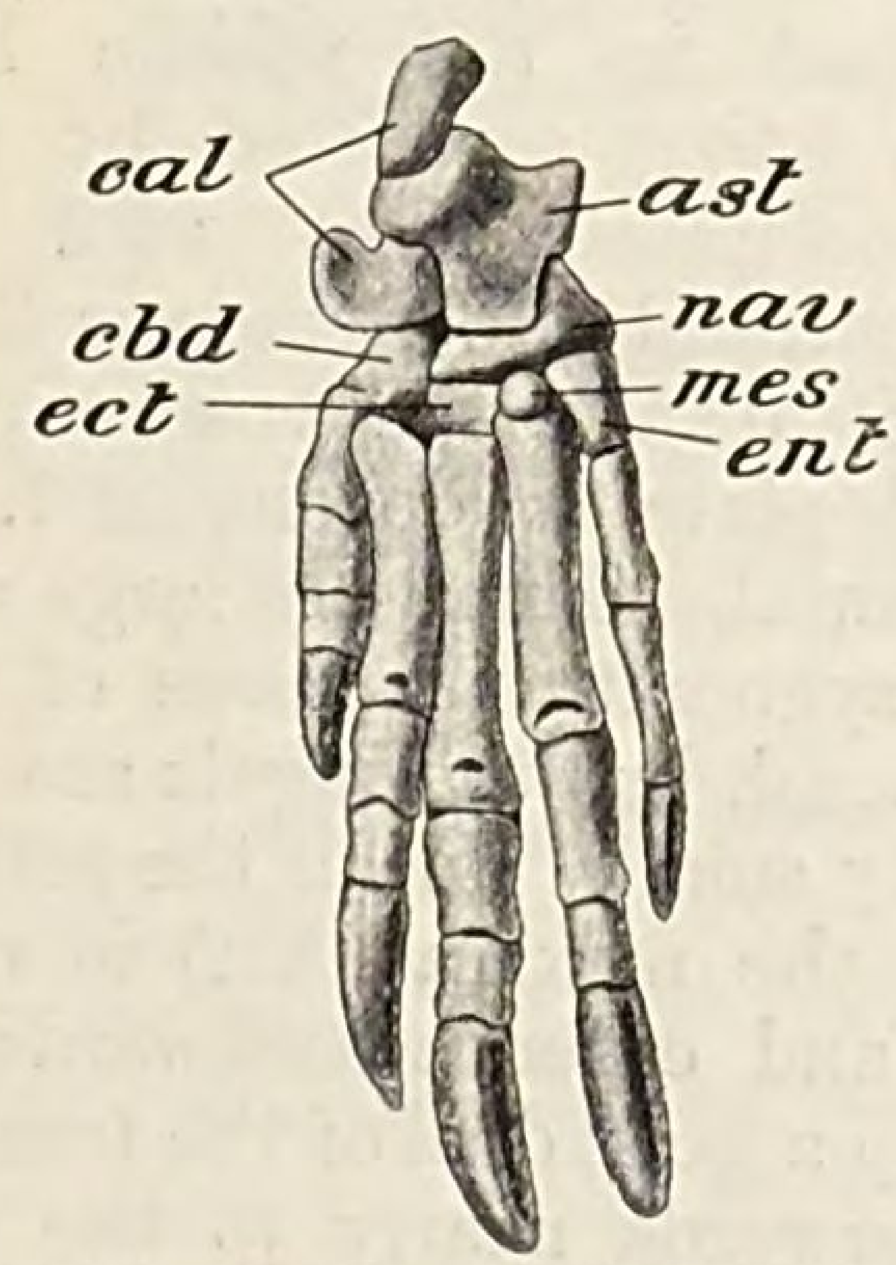


Fig. 1078.—Pes of **Armadillo** (*Dasypus sexcinctus*). *ast.* astragalus; *cal.* calcaneum; *cbd.* cuboid; *ect.* ecto-cuneiform; *ent.* ento-cuneiform; *mes.* meso-cuneiform; *nav.* navicular.

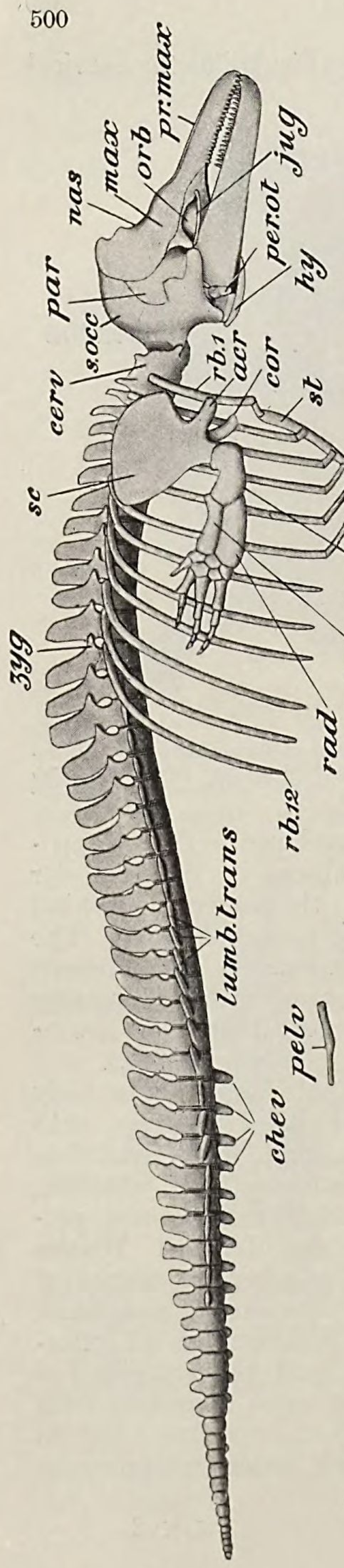


FIG. 1079.—Skeleton of **Porpoise** (*Phocæna communis*). *acr.* acromion process of scapula; *cerv.* united cervical vertebræ; *chev.* chevron bones; *cor.* coracoid process; *hu.* humerus; *hy.* hyoid; *jug.* jugal; *lumb. trans.* lumbar transverse processes; *max.* maxilla; *nas.* nasal; *orb.* orbit; *par.* parietal; *pelv.* vestige of pelvis; *per. ot.* periotic; *pr.max.* pre-maxilla; *rad.* radius; *rb1.* first rib; *rb12.* twelfth rib; *sc.* scapula; *s. occ.* supra-occipital; *st.* sternum; *uln.* ulna; *zyg.* pre-zygapophysis.

The *sternum* varies in shape. Sometimes it consists of a pre-sternum and a series of several sternebræ without xiphisternum; sometimes (Fig. 1080) it is a con-

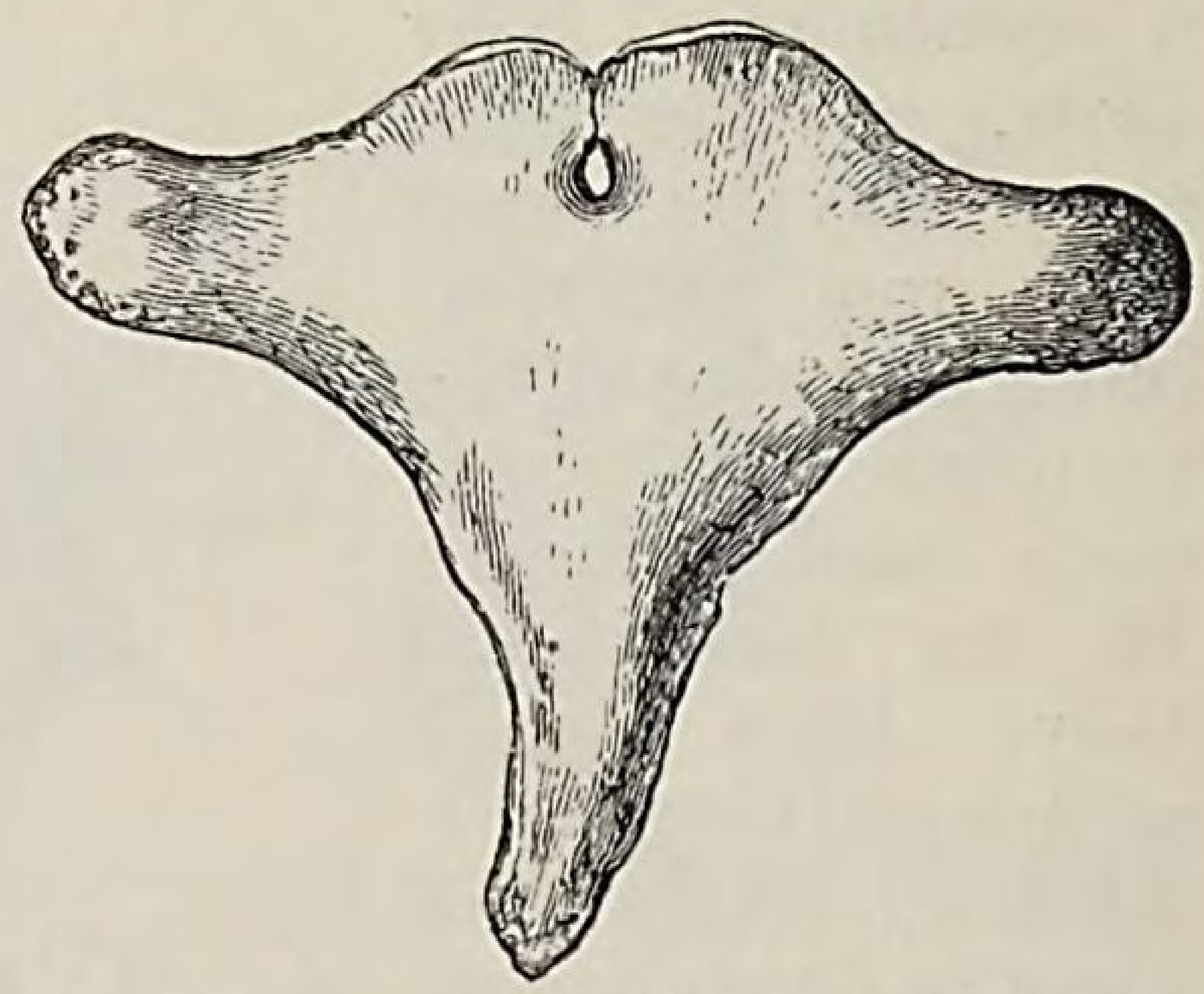


FIG. 1080.—Sternum of **Roqual** (*Balænoptera musculus*). (After Flower.)

tinuous plate of bone, occasionally with median notches or fontanelles.

In the *skull* (Fig. 1081) the brain-case is rounded, the jaws greatly elongated, often unsymmetrical. The parietals (*Pa.*) do not meet in the middle line above, being separated by the supra-occipital (*SO.*) with an inter-parietal (*IP.*); there is thus no sagittal suture. A large supra-orbital plate is developed from the frontal. There are large and stout zygomatic processes of the squamosal, but the jugals are extremely small. In all the recent forms the maxilla (*Mx.*) is very large and extends backwards to overlap a good deal of the frontal, and forwards nearly to the extremity of the snout; while the premaxillæ (*P. Mx.*), which are long narrow bones, bound but a very small part of the oral border of the upper jaw. The nasals (*Na.*) are very small. The tym-

panic bone is very large, and is sometimes fused with the periotic (Mystaceti) sometimes not (Odontoceti). The lower jaw is remarkable for the absence of an ascending ramus.

The *scapula* in most of Cetacea is very broad and flat, expanded into the shape of an open fan. The spine is usually situated close to the anterior border, sometimes coalescent with it. The acromion is curved and flat, the coracoid also compressed and parallel with the acromion. In some, both acromion and coracoid are absent. There is never any trace of a clavicle. The humerus is short and

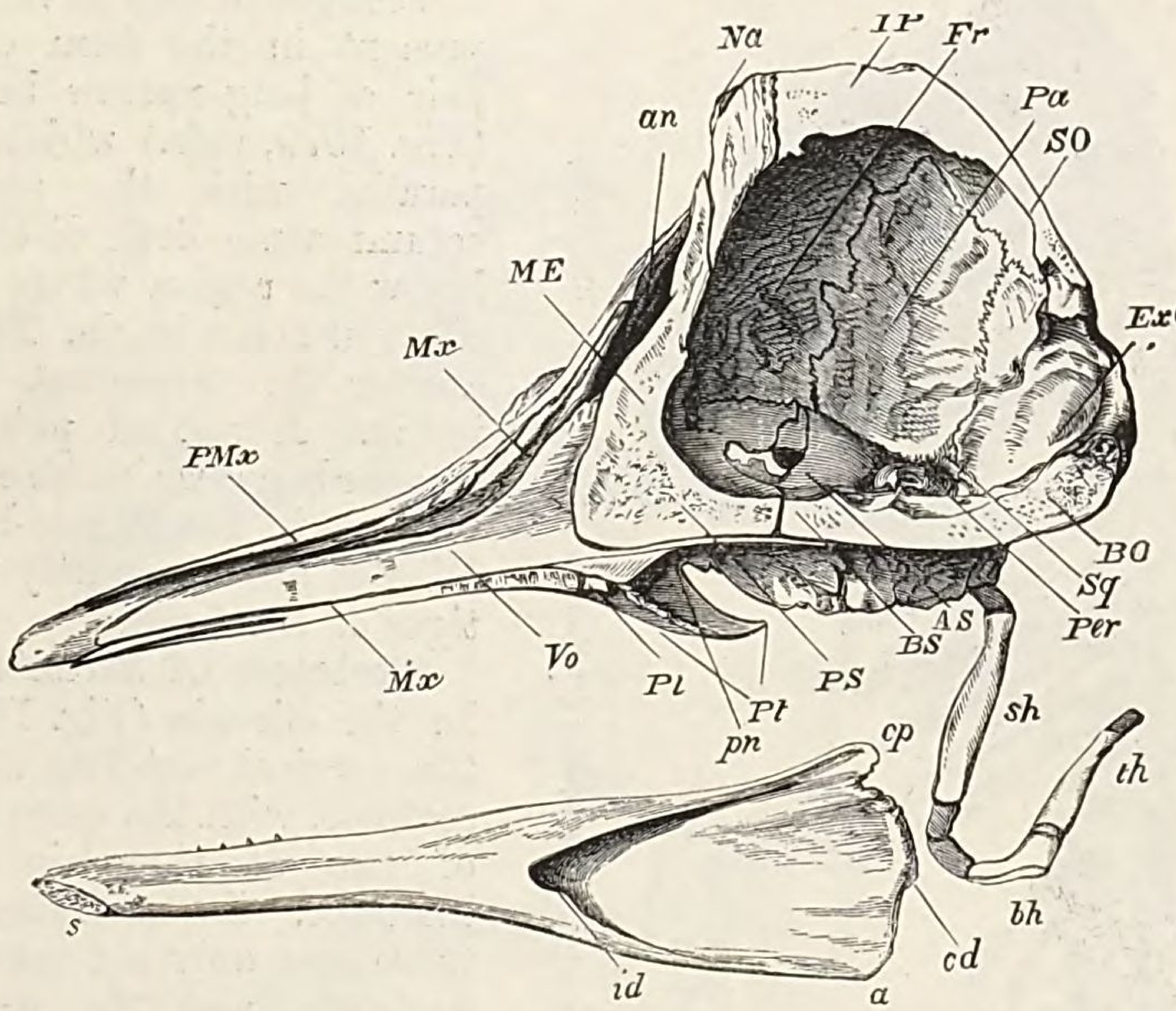


FIG. 1081.—Skull of **Dolphin** (*Globiocephalus*), sagittal section. *an.* external nares; *bh.* basi-hyal; *BO.* basi-occipital; *BS.* basi-sphenoid; *cd.* condyle of mandible; *cp.* coronoid process; *EO.* ex-occipital; *Fr.* frontal; *IP.* inter-parietal; *ME.* mesethmoid; *Mx.* maxilla: *Na.* nasal; *Pa.* parietal; *Per.* periotic; *Pl.* palatine; *P.Mx.* pre-maxilla; *pn.* posterior nares; *PS.* presphenoid; *Pt.* pterygoid; *sh.* stylo-hyal; *SO.* supra-occipital; *Sq.* squamosal; *th.* thyro-hyal; *Vo.* vomer. (After Flower.)

very stout; the head freely movable in the glenoid cavity; the distal articulating surfaces are flat and oblique, meeting at an angle. The proximal ends of the radius and ulna are so firmly united as to allow of very little movement; at the distal end there are no synovial membranes. The manus is extremely modified. There are no synovial joints; the carpus is in some (Whale-bone Whales) almost entirely cartilaginous, as also are the metacarpals and phalanges—the cartilages being coalescent or separated by intervals of fibrous tissue: in some of the carpal elements bone is deposited. In the toothed Whales the carpal bones are completely ossified, and are of polygonal form: the phalanges are also ossified, with incomplete

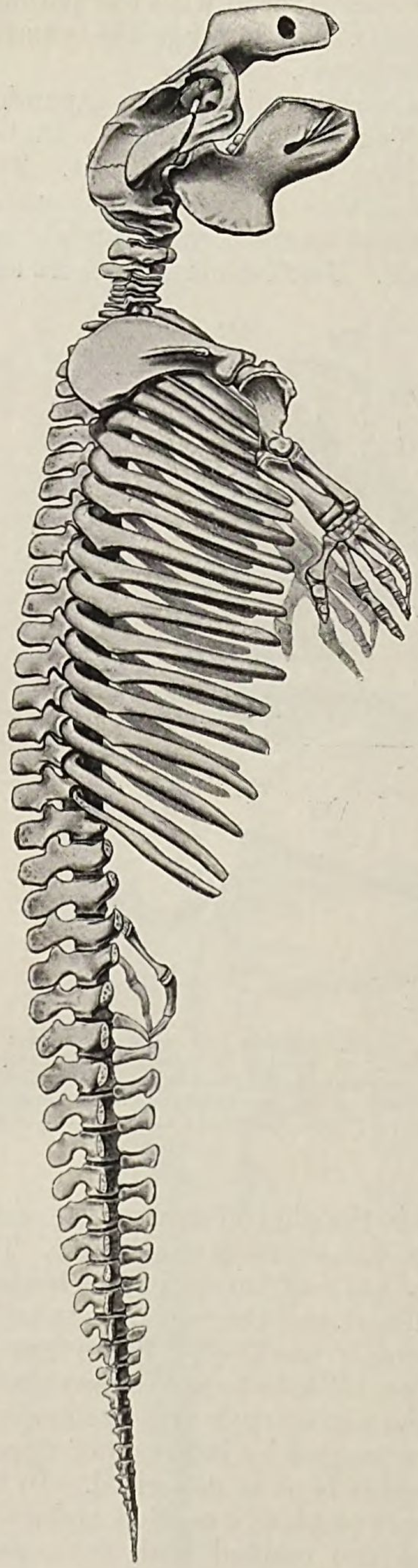


Fig. 1082.—Skeleton of **Dugong** (*Halicore australis*). (After Blainville.)

synovial articulation. In the Cetacea there are sometimes five digits, sometimes only four: more or fewer have considerably more than the normal number of phalanges, sometimes as many as fourteen. The second is usually the longest.

Vestiges of the *pelvis* are present in the form of a pair of long narrow bones (Fig. 1079, *pelv.*) which lie parallel with the spinal column some little distance below the region where the chevron bones begin. These appear to represent the ischia. A second pair of smaller bones which lie close to these in the Whale-bone Whales are apparently vestiges of the femora.

Skeleton of Sirenia.—In the Sirenia (Fig. 1082) the cervical vertebræ never coalesce, with the exception of two of them in the Manatee. In the Manatee there are only six cervical vertebræ, and the neural arches are sometimes incomplete. In the trunk the thoracic vertebræ are numerous; all have well-developed facets for the heads of the ribs, and well-developed zygapophyses. The caudal vertebræ are numerous, depressed, with wide transverse processes. The ribs are numerous, but few of them are connected with the sternum. The sternum is a broad bone not composed of distinguishable segments.

The *skull* (Fig. 1083) is characterised by its extreme hardness. The cranial cavity is rather long and narrow as compared with that of the Cetacea. Although the supra-occipital (*SO.*) is produced forwards on the upper surface of the skull for a considerable distance, it does not separate the parietals (*Pa.*) from one another. The frontal develops broad supra-orbital plates. The zygoma is stout. As in the Cetacea the external nares are very wide, but are relatively further forwards. The nasals are rudimentary. The tympanic and periotic are readily separable from the other

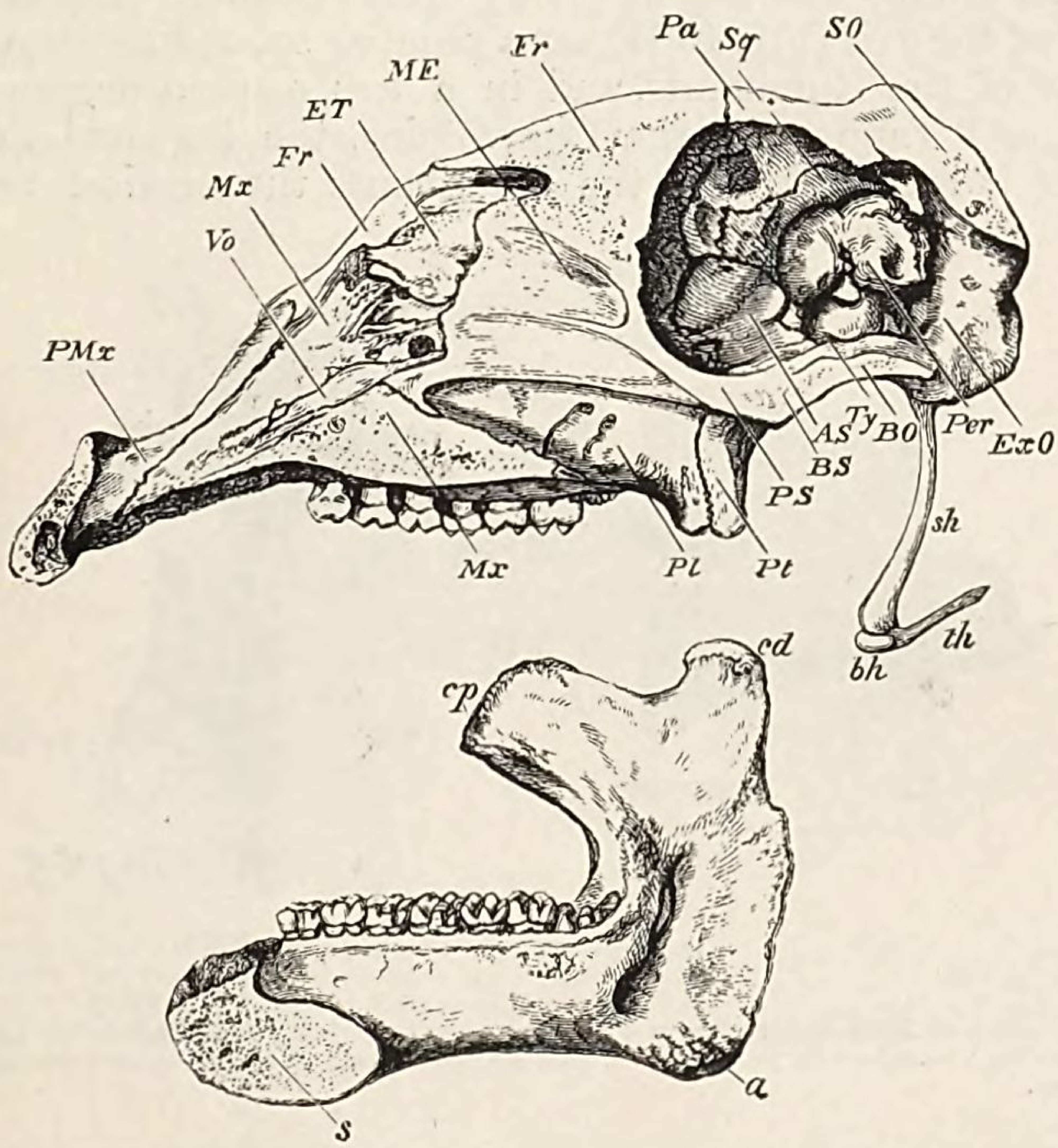


FIG. 1083.—Section of skull of **Manatee** (*Manatus senegalensis*). Letters as in Fig. 1081. In addition, *ET.* ethmo-turbinal; *Ty.* tympanic. (After Flower.)

bones. There are enormous pre-maxillæ in the Dugongs. The mandible has a well-developed ascending ramus and coronoid process (*cp.*).

The *scapula* of the Sirenia is much more like that of the terrestrial Mammals than is that of Cetacea, but is nearer that of the Seals; it is narrow and curved backwards. The spine is situated about the middle; the acromion is directed downwards. The coracoid is fairly well developed, and of a conical shape. The clavicle is absent, as in the Cetacea. The skeleton of the arm also departs less from the ordinary Mammalian type than in the Cetacea. The

radius and ulna are ankylosed at their extremities. The carpus has seven bones in the Manatee: the pisiform is absent. In Dugong coalescence takes place between the carpal bones, so that the number of ossifications is reduced in the adult. There are five digits, all of which possess the normal number of phalanges.

The *pelvis* is represented by a pair of vestiges widely separated from the spinal column, and having a vertical position: they probably represent the ilia.

Skeleton of the Ungulata.—In general the centra of the Ungulata are more or less distinctly opisthocœlous. The odontoid process of the axis (Fig. 1084) has a peculiar spout-like form in the majority of the Ruminants, and in a less marked degree in the Horses and Tapirs: in the Chevrotains, the Pigs and the Proboscidea it is conical. In the Ruminants the cervical vertebræ

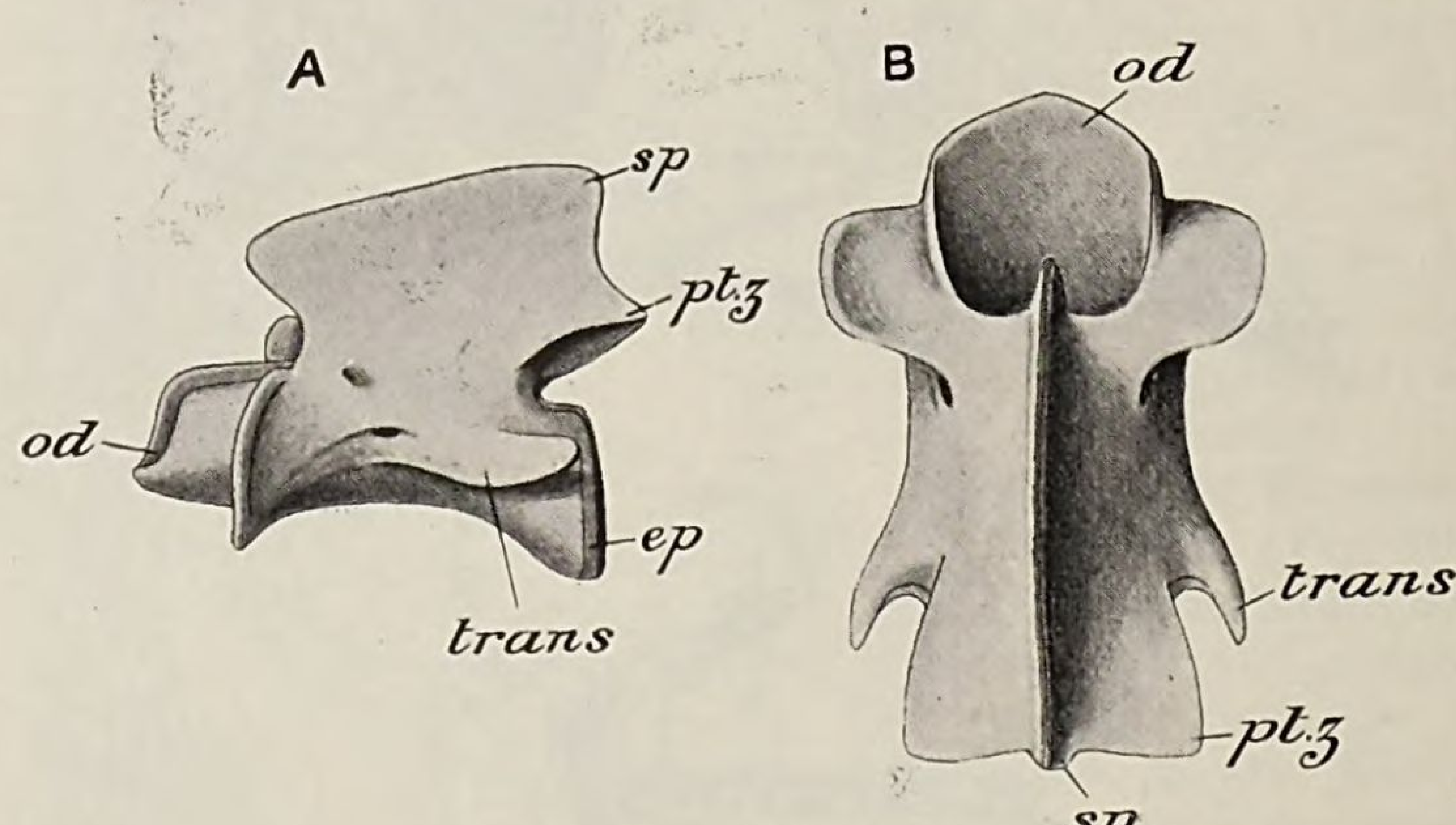


FIG. 1084.—Axis of **Red Deer** (*Cervus elaphus*). *A*, lateral view; *B*, dorsal view. *ep.* epiphysis of centrum; *od.* odontoid process; *pt.z.* post-zygapophysis; *sp.* neural spine; *trans.* transverse process.

present a median keel below, produced in the posterior part of the region into a process. The development of the cervical neural spines varies: in most they are elongated and compressed; but in the Horses they are almost completely absent, and in the Elephants they are all small, with the exception of the last. The number of thoracico-lumbar vertebræ is nearly always nineteen in the Artiodactyles, twenty-three in the Perissodactyles and in the Proboscidea. Hyrax has a larger number of trunk vertebræ—twenty-eight to thirty—than any other terrestrial Mammal. The transverse processes of the lumbar vertebræ are nearly always elongated, flattened, and directed outwards, or outwards and slightly forwards. Usually there is a single wide sacral vertebra united with the ilia, ankylosed with which behind are a varying number

of narrow vertebræ. There are never chevron bones in the caudal region of any existing Ungulate.

In all the Ungulata the sternebræ are distinct. As a general rule the pre-sternum is narrow, sometimes (Horses and Tapirs) greatly compressed laterally, while the meso-sternum is broad; but in the Rhinoceros the meso-sternum is no broader than the pre-sternum.

Among the Perissodactyle Ungulates the *skull* of the Horse (Fig. 1085) is elongated, especially in the facial region; the axis of the skull, or the line from the anterior margin of the pre-maxillæ to the lower edge of the foramen magnum, is nearly straight, and both the occipital plane and ethmoidal plane are nearly perpendicular to it. The supra-occipital (*SO.*) has a prominent transverse crest; and in front of this the temporal ridges which limit the tem-

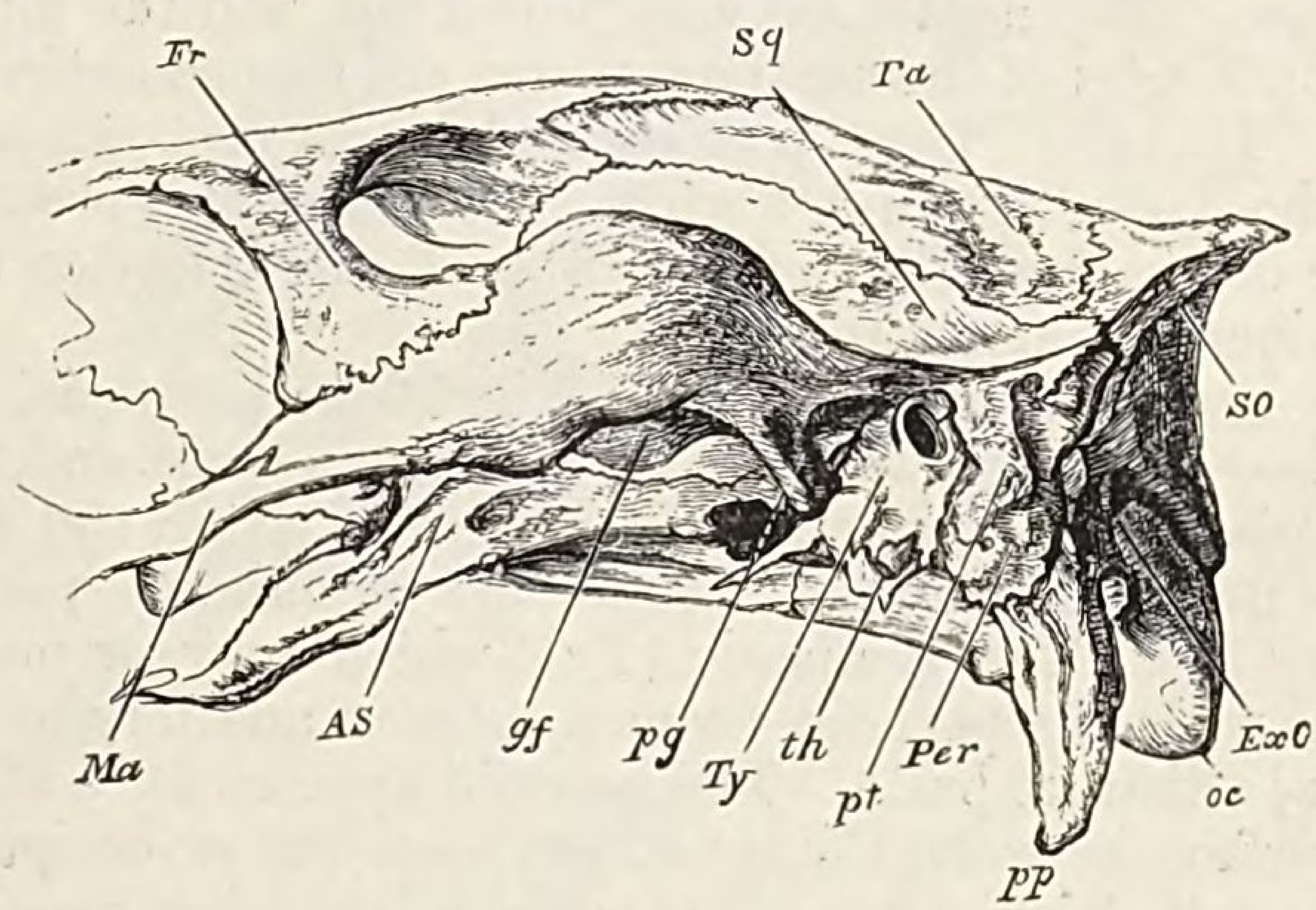


FIG. 1085.—Side view of posterior parts of skull of **Horse** (*Equus caballus*). *AS.* alisphenoid; *Fr.* frontal; *g. f.* glenoid fossa; *Ma,* jugal; *oc.* occipital condyle; *Pa.* parietal; *pp.* par-occipital process; *Per.* periotic; *p. g.* post-glenoid process of squamosal; *p.t.* post-tympanic process; *SO.* supra-occipital; *Sq.* squamosal; *t. h.* tympanic hyal; *ty.* tympanic. (After Flower.)

poral fossa above, unite to form a median longitudinal *sagittal crest*, running along the course of the sagittal sutere. The ex-occipital develops prominent, downwardly-directed, par-occipital process (*pp*). The tympanic (*Ty.*) is small and, with the periotic (*Per.*), is only loosely connected with the neighbouring bones, being held in place mainly by a post-tympanic process developed from the squamosal. A considerable part of the periotic (mastoid portion) appears on the surface of the skull between this and the ex-occipital. The tympanic forms a tubular auditory meatus, but is not expanded into a bulla. The glenoid fossa is extended transversely, and is bounded behind by a post-glenoid process. The orbit, which is relatively small, is completely surrounded by bone. The nasals are large, and are separated from the pre-maxillæ in a great part of their extent. The mandible has a large ascending ramus, and a

coronoid process which rises high above the level of the condyle; the latter is elongated transversely in co-ordination with the form of the glenoid cavity.

The skull of the Rhinoceros differs from that of the Horse mainly in the presence of large air-cells in the supra-occipital and parietal bones, and in the orbit not being separated by bone from the temporal fossa. The post-glenoid process equals or exceeds the par-occipital; the mastoid does not appear on the surface, owing to the post-tympanic process of the squamosal extending backwards to articulate with the ex-occipital and concealing it from view.

The skull of the Tapirs resembles that of the Rhinoceros in most respects. As in the latter, the orbits are not completely bounded by bone behind. The nasal openings are very large, and extend backwards above the orbits, separated from them only by a thin plate. The nasals are very prominent, and the inferior and lateral boundaries of the nasal apertures are formed entirely by the maxillæ. There are large post-glenoidal and post-tympanic processes; the latter is united with the par-occipital process. The mandible differs from that of the other Perissodactyles chiefly in the prominent incurved angle.

In the Ruminant Artiodactyles (Fig. 1086) the facial region is more or less bent downwards on the basi-cranial axis, and, while the occipital plane is nearly perpendicular to the latter, the ethmoidal plane is nearly horizontal. There are prominent par-occipital processes (*pp*). The tympanic (*Ty*), which may or may not be ankylosed with the periotic, forms a tubular auditory meatus and sometimes a distinct bulla. The mastoid appears for a short space on the surface, between the squamosal and the ex-occipital. The frontals usually bear a pair of processes, more or less prominent, for the support of the horns, and between these a transverse ridge frequently extends. The orbit is completely encircled by bone, and has a prominent margin. The nasals are elongated and the pre-maxillæ slender. The condyle of the mandible is broad and flat; the horizontal ramus usually rather slender, and expanded in front for the lodgment of the incisors.

In the Pigs, as in the Ruminants, the facial region is bent downwards. There is a prominent transverse occipital crest at the junction of the supra-occipital and parietals; but the temporal ridges do not meet in the middle to form a sagittal crest such as occurs in the skull of the Horse. There are prominent par-occipital processes. There is a large, but compressed, bulla tympani; the auditory meatus is very long, directed upwards and outwards, and is surrounded by the post-glenoidal and post-tympanic processes, which are in contact with one another. The mastoid is rudimentary, and does not appear on the outer surface of the skull. The frontal develops a short post-orbital process; but this does not meet the zygoma, so that the bony margin of the orbit is

incomplete behind. The facial region as a whole is elongated and laterally compressed. The nasals are long and narrow, and the pre-maxillæ send backwards long processes on each side of them. A peculiar bone—the *pre-nasal*—is developed in the nasal septum. The condyle of the mandible is transversely elongated; the coronoid process very small.

The skull of the Hippopotamus differs from that of the Pig mainly in the proportions of the various parts. The cranial cavity

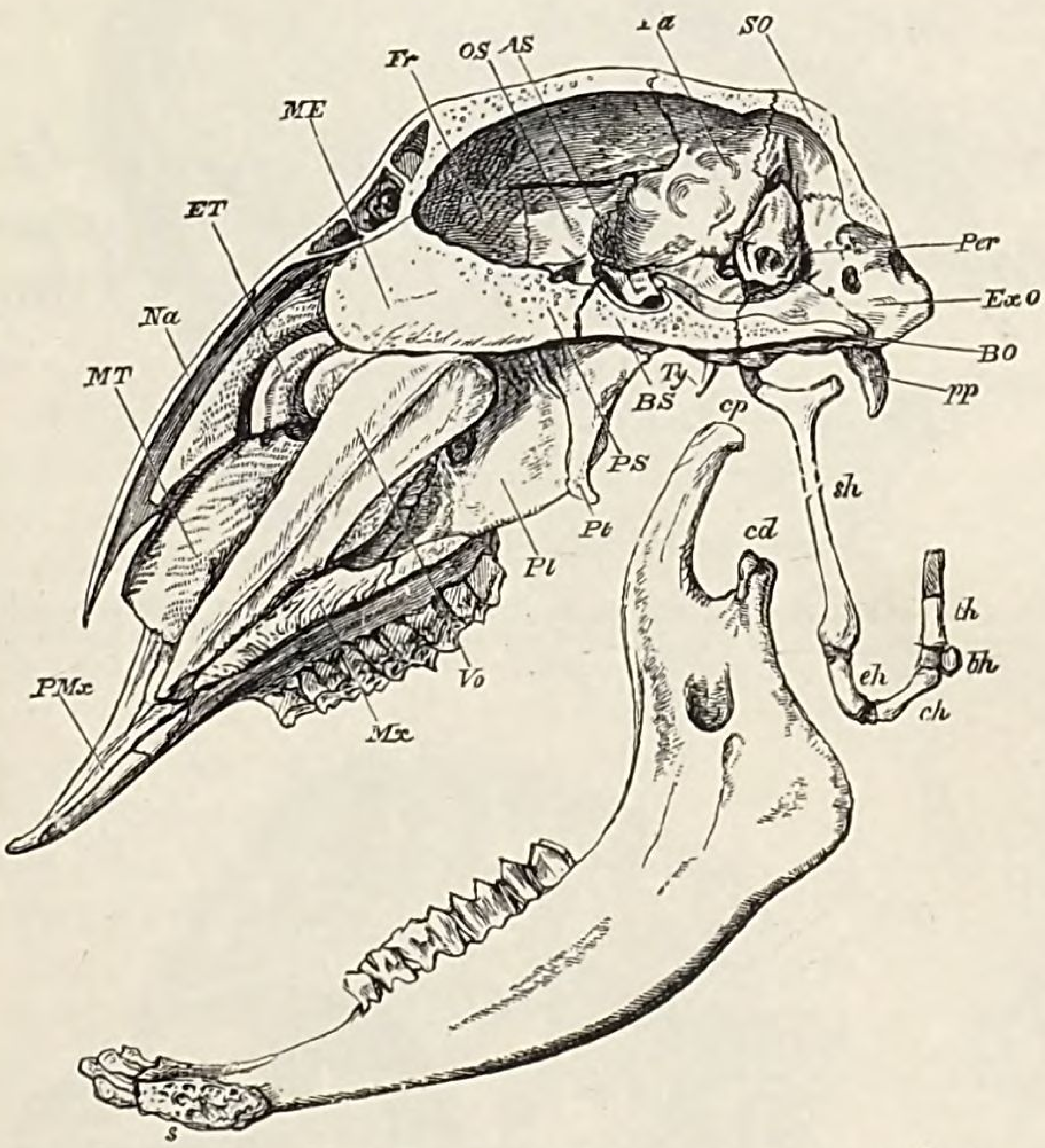


FIG. 1086.—Section of skull of **Sheep** (*Ovis aries*). *AS.* alisphenoid; *BO.* basi-occipital; *BS.* basi-sphenoid; *EO.* ex-occipital; *ET.* ethmo-turbinal; *Fr.* frontal; *ME.* mesethmoid; *MT.* maxillary turbinal; *Mx.* maxilla; *Na.* nasal; *OS.* orbito-sphenoid; *Pa.* parietal; *Pl.* palatine; *Per.* periotic; *P.Mx.* pre-maxilla; *P.S.* pre-sphenoid; *Pt.* pterygoid; *s. h.* stylo-hyal; *SO.* supra-occipital. (After Flower.)

is relatively small, and the face large. The orbits are almost tubular, and are almost, or quite, encircled by bone. The face is laterally contracted in front of the orbit and again expands anteriorly. The mandible is extremely massive; anteriorly the symphysial portion is greatly expanded to support the large incisor and canine teeth.

In the Hyracoidea (Fig. 1087) the skull shows affinities with Rodents and also with Perissodactyles. The zygomatic arch is stout: it is formed mainly by the jugal (*ju*), which forms part of the glenoid fossa. The post-orbital processes meet in some to bound

the orbit behind; the upper is formed from the parietal (*par*). The facial region is comparatively short. The pre-maxillæ (*p. max*) are not greatly developed. There are distinct par-occipital processes (*p. oc.*). The periotic and tympanic are ankylosed together,

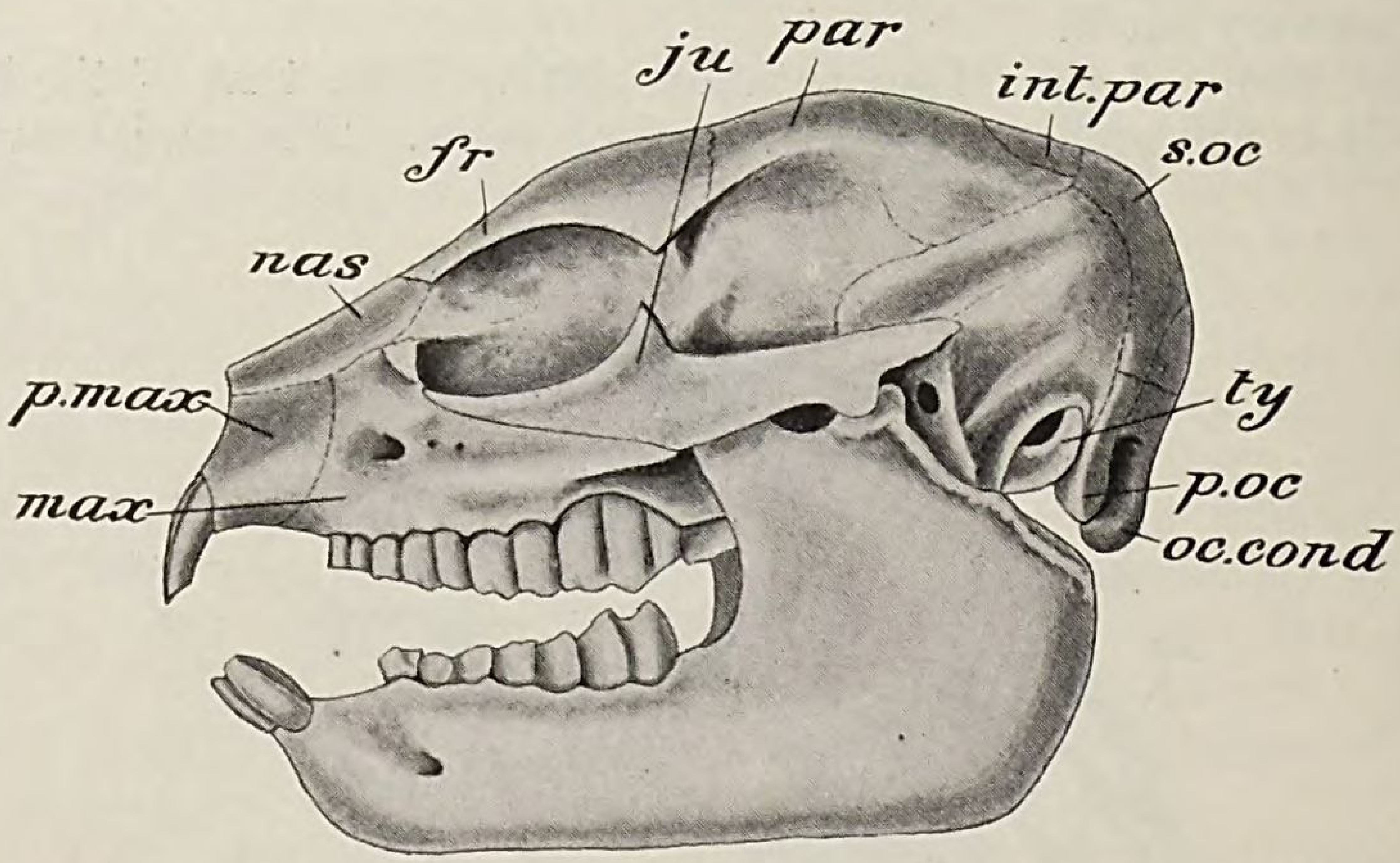


FIG. 1087.—Skull of **Hyrax.** Letters as in Fig. 1063, p. 491; in addition, *int. par.* interparietal; *ty.* tympanic. The suture between the frontal and parietal has been by an error made to run behind the post-orbital process.

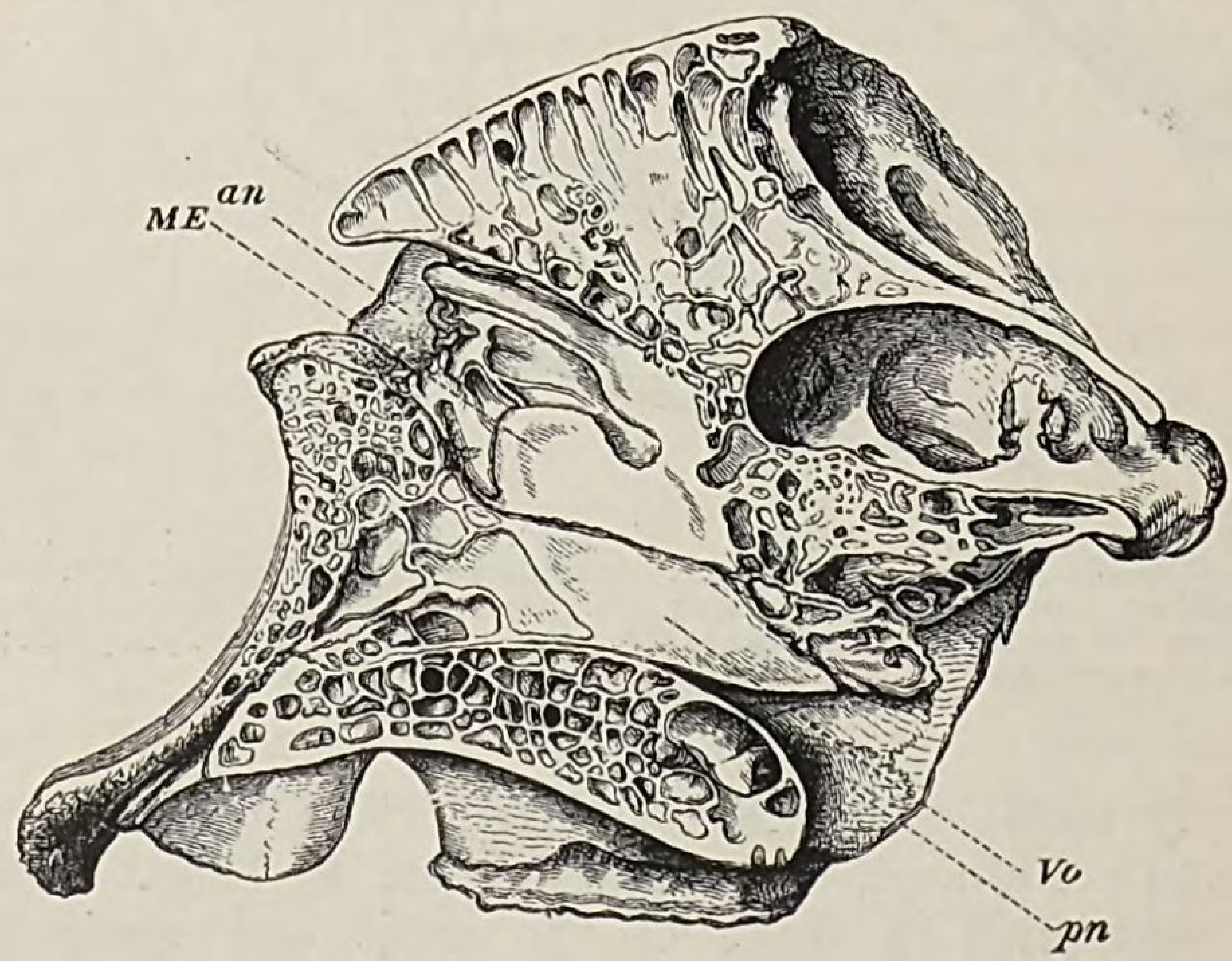


FIG. 1088.—Section of skull of **African Elephant** (*Elephas africanus*), to the left of the middle line. *a. n.* anterior nares; *ME.* mesethmoid; *p. n.* posterior nares; *Vo.* vomer. (After Flower.)

but not to the squamosal. The tympanic (*ty.*) forms a bulla with a spout-like prolongation.

In the Proboscidea (Fig. 1088) the bones of the skull are of enormous thickness, the inner and outer tables being separated by

extensive air-cells. The sutures are early obliterated. Paroccipital and post-glenoidal processes are absent. The tympanic forms a large, rounded auditory bulla; but the external auditory meatus is bounded chiefly by the post-tympanic process of the squamosal. The mastoid portion of the periotic does not appear on the surface. The orbit is not completely separated by bone from the temporal fossa. The nasal aperture is situated far back, and looks upwards and forwards almost as in the skull of some of the Cetacea. The chief characteristic of the mandible is its prolongation forwards with a spout-like process at the symphysis.

In the Ungulata vera the *scapula* (Fig. 1089) is never very broad; the spine is usually near the middle. Neither the acromion nor the coracoid process is very prominent; sometimes, as in the Horse, the former is absent. A clavicle is never present. In the Ruminants the vertebral portion of the scapula remains cartilaginous, forming the so-called *supra-scapular cartilage* (*ss*). In Pigs and some Perissodactyles, though there is no acromion, there is a triangular process about the middle of the spine.

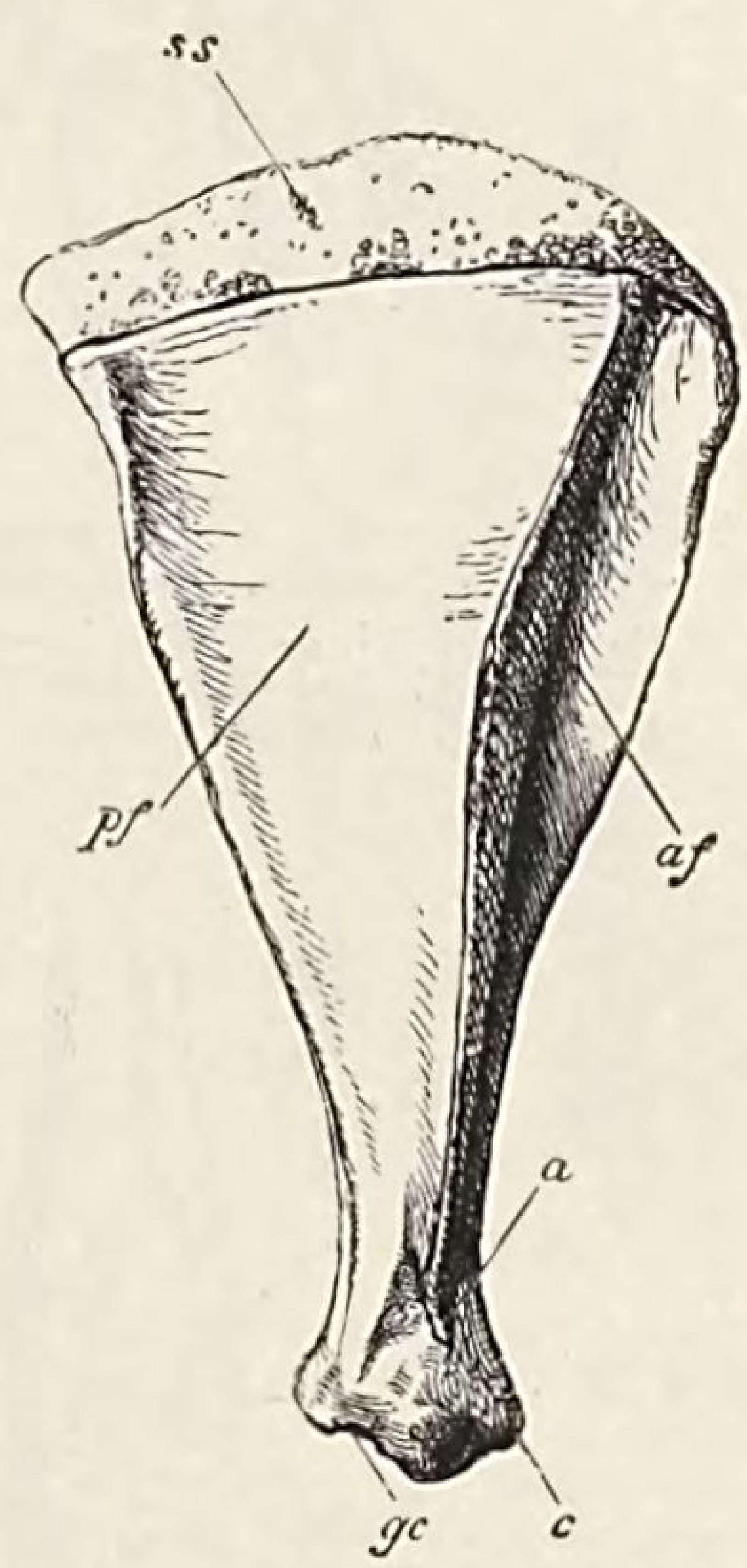


FIG. 1089.—Right scapula of **Red Deer** (*Cervus elaphus*). *a.* acromion; *af.* prescapular fossa; *c.* vestigial coracoid process; *gc.* glenoid cavity; *pf.* post-scapular fossa; *sp.* spine; *ss.* imperfectly ossified suprascapular portion. (After Flower.)

The humerus is short and stout, the radius is always well developed, the ulna is in some (Pigs, Hippopotami, Tapirs, and Rhinoceroses) well developed, in others (the Horses and the Ruminants) it is incomplete.

The first digit is always absent. There is never a centrale. The trapezium and magnum unite in most of the Ruminants.

In the Perissodactyla the third digit in both the fore and hind foot is symmetrical in itself. In the Rhinoceroses the second and fourth are also present, and in the Tapirs (Fig. 1090) the fifth of the fore-foot is developed as well. The Horses (Fig. 1091) present the greatest reduction in the number of the digits observable in any Mammal, the third being the only functional digit in each foot. Its elongated metacarpal or metatarsal (*cannon bone*) has in apposition with it laterally a pair of splint-like vestiges which represent the metacarpals or metatarsals of the second and fourth digits. In the Artiodactyla, on the other hand, the third and fourth digits form a symmetrical pair. In the Ruminant Artiodactyles (Fig. 1093) the metacarpals

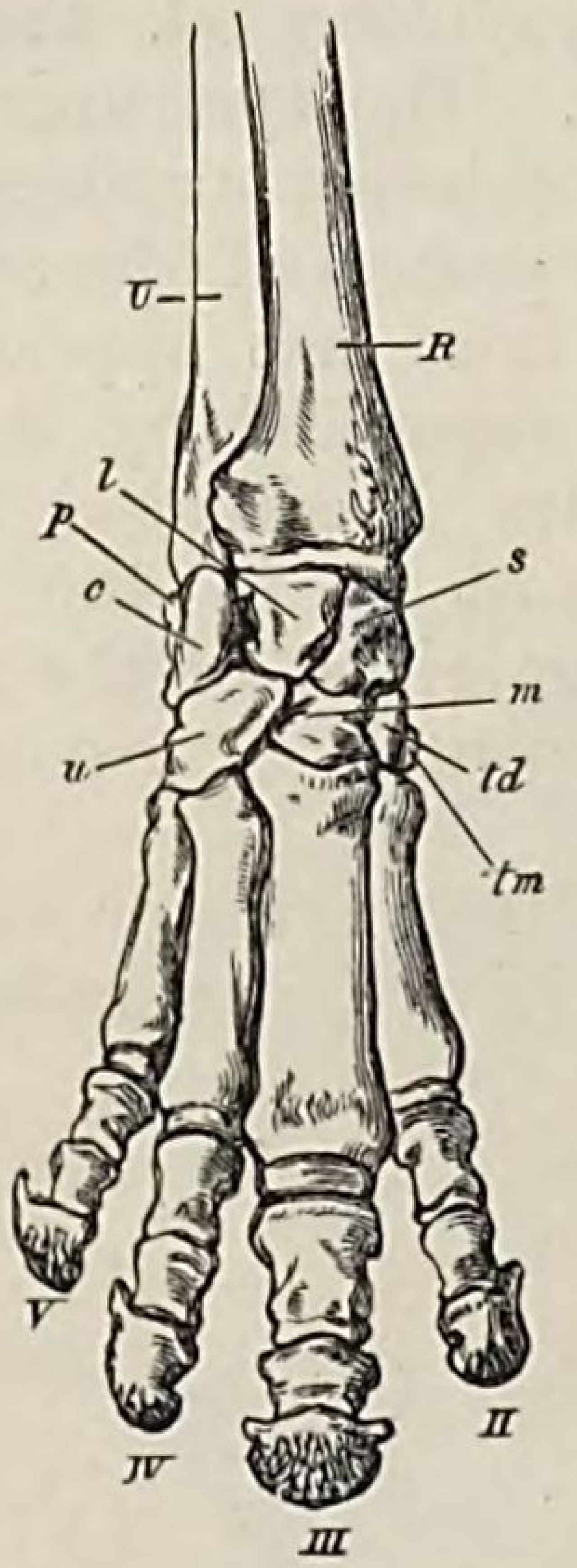


FIG. 1090.—Bones of the manus of **Tapir** (*Tapirus indicus*). *c.* cuneiform; *l.* lunar; *m.* magnum; *R.* radius; *s.* scaphoid; *td.* trapezoid; *tm.* trapezium; *U.* ulna; *u.* unciform. (After Flower.)

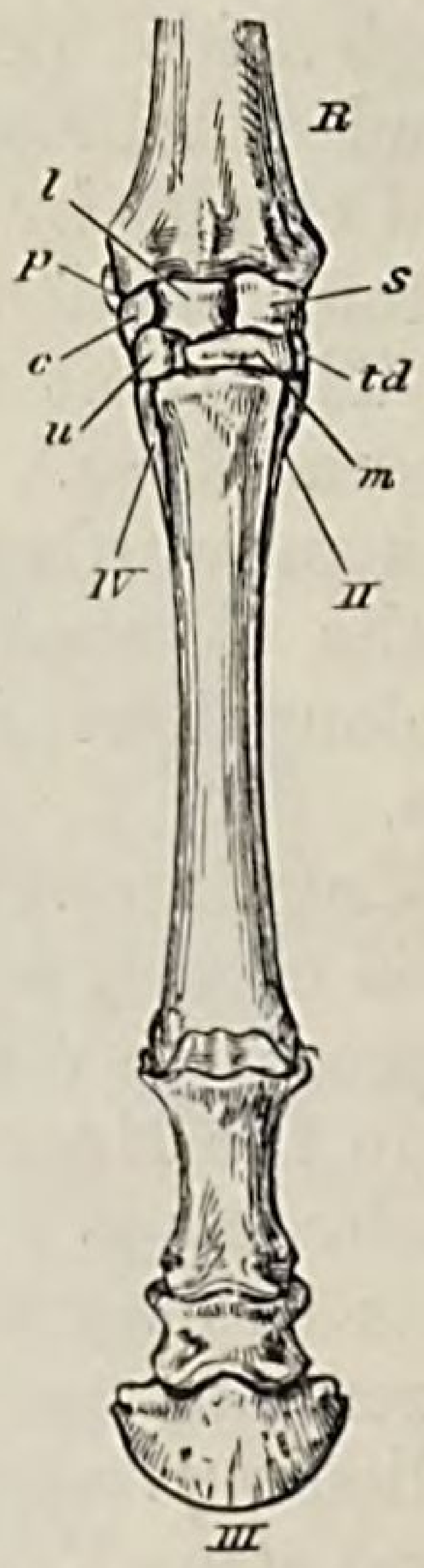


FIG. 1091.—Bones of the manus of **Horse** (*Equus caballus*). *c.* cuneiform; *l.* lunar; *m.* magnum; *R.* radius; *s.* scaphoid; *td.* trapezoid; *u.* unciform; *II*, *IV*, vestigial second and fourth metacarpals. (After Flower.)

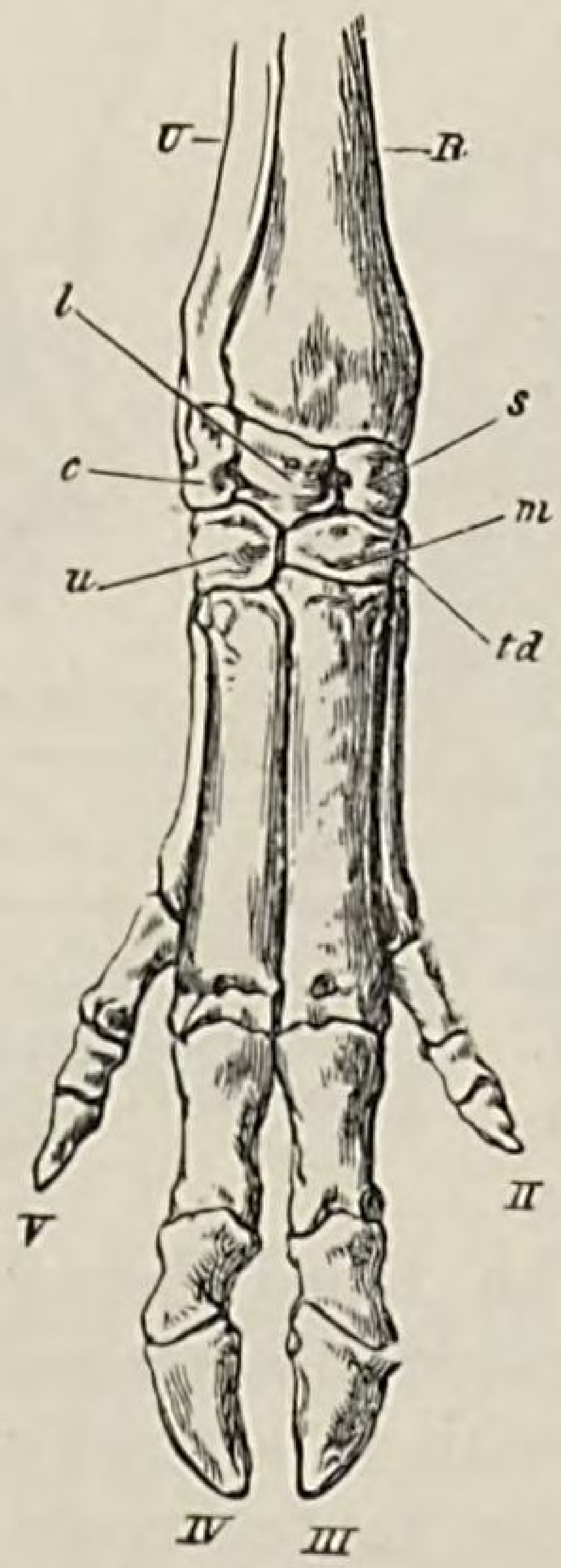


FIG. 1092.—Bones of manus of **Pig** (*Sus scrofa*). *c.* cuneiform; *l.* lunar; *m.* magnum; *s.* scaphoid; *td.* trapezoid; *tm.* trapezium; *u.* unciform. (After Flower.)

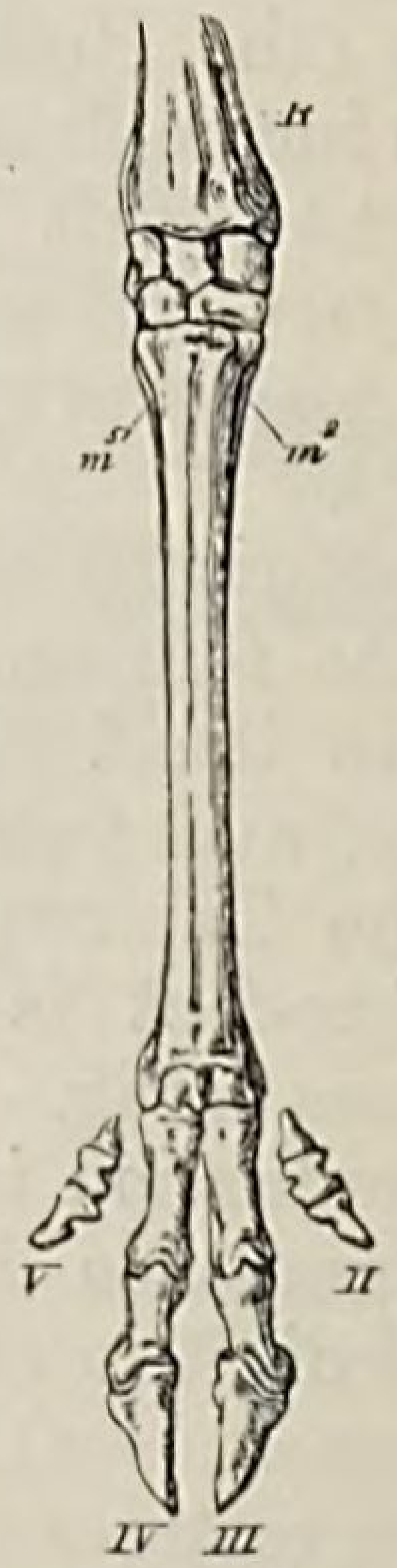


FIG. 1093.—Bones of manus of **Red Deer** (*Cervus elephas*). m^2. m^5. vestigial second and fifth metacarpals. *R.* radius. (After Flower.)

or metatarsals of these digits unite to form a single elongated bone, the *cannon bone.*

The *pelvis* of most Ungulata is greatly elongated. The ilia are wide transversely, the symphysis is very long, involving a part of the ischia as well as the pubes. In the Perissodactyla, but not in the Artiodactyla, there is a well-marked third trochanter.

In some Ungulates (Rhinoceroses, Tapirs, Pigs, Hippopotami), the fibula is distinct though slender. In the Horse it is represented by a vestige. In the Ruminants it is represented only by a small

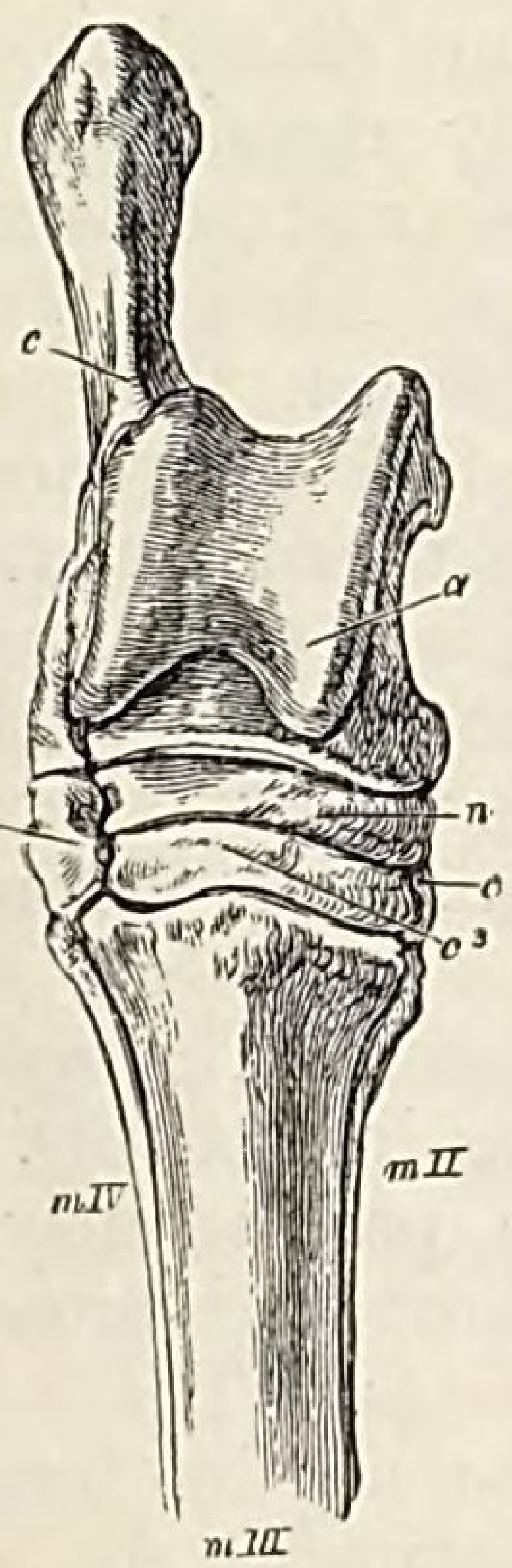


FIG. 1094.—Dorsal surface of right tarsus of **Horse** (*Equus caballus*). *a.* astragalus; *c.* calcaneum; *cb.* cuboid; c². united meso- and ento-cuneiform; *c³.* ecto-cuneiform; *n.* navicular; *s.* scaphoid; *II*, *IV*, vestigial second and fourth metatarsals; *III*, third metatarsal. (After Flower.)

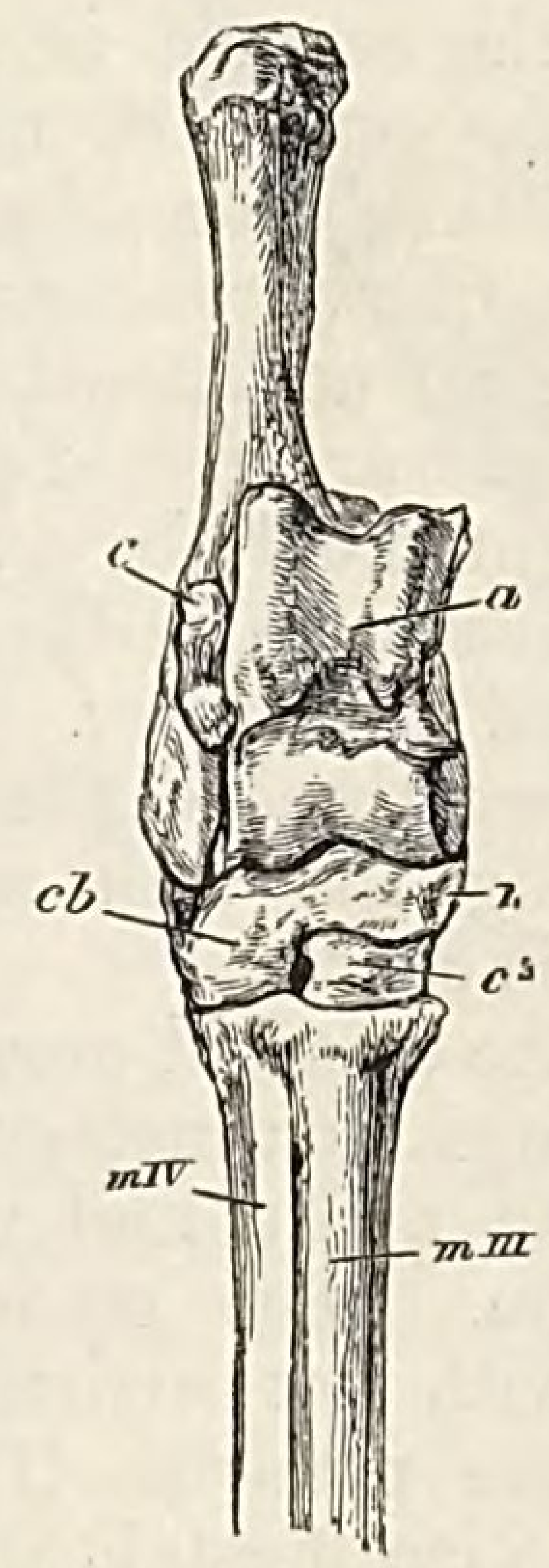


FIG. 1095.—Dorsal surface of right tarsus of **Red Deer** (*Cervus elaphus*). *a.* astragalus; *c.* calcaneum; *cb.* cuboid; *c³.* conjoined ecto- and meso-cuneiforms; mt_3. mt_4. third and fourth metatarsals; *n.* navicular. (After Flower.)



FIG. 1096.—Dorsal surface of right tarsus of **Pig** (*Sus scrofa*). *a.* astragalus; *c.* calcaneum; *cb.* cuboid; c³. ecto-cuneiform; c². meso-cuneiform; *m.* metatarsals; *n.* navicular. (After Flower.)

vestige, the *malleolar bone,* which articulates with the distal end of the tibia.

The structure of the foot exhibits a close parallelism to that of the manus. The tarsal bones are closely dove-tailed together, and articulate with one another by flat surfaces. The hallux is never developed. In the Perissodactyla the third digit is symmetrical in itself. In the Rhinoceros and Tapirs the second and fifth digits are also completely developed; but in the Horses (Fig. 1094) they are represented only by splint-like vestiges of their metatarsals, the metatarsal of the third digit forming an

elongated *cannon bone*, like the metacarpal of the third digit of the manus. In the Rhinoceroses and Tapirs all the usual tarsal bones are present; in the Horses the ento-cuneiform and meso-cuneiform are united. In the Artiodactyles the third and fourth digits form a symmetrical pair as in the manus; and in the Ruminants (Fig. 1095) their metatarsals unite to form a cannon bone. In most Ruminants there are no vestiges of the second and fifth digits. In the Pigs (Fig. 1096) all the tarsal bones are present. In most Ruminants the cuboid and navicular are united; in the Camels these bones are distinct, but the ento-cuneiform is wanting.

In the Hyracoidea the scapula is triangular, like that of the Ungulata vera, and the spine is moderately developed, most prominent in the middle. There is a large supra-trochlear foramen. The radius and ulna are complete, but often ankylosed. In the carpus there is an additional bone between the scaphoid and the trapezoid. There are five digits, the first very small; in some the last is represented only by a rudimentary metacarpal.

In the femur an indistinct ridge-like elevation is to be regarded as representing the third trochanter. The foot resembles that of the Rhinoceros in having three digits developed; but there is a small bone representing the fifth metatarsal, and the ungual phalanx of the second is cleft.

In the Proboscidea the coracoid process is small. The acromion presents a recurved process or metacromion, as in Rodents. The clavicle is absent. The radius and ulna are permanently fixed in the prone condition. The manus is short and broad, the carpals are squarish, with flat articular surfaces. There is no centrale; five digits are present. The pelvis has its long axis nearly vertical. The iliac crest is directed transversely, and is greatly expanded; the iliac and gluteal surfaces look almost directly forwards and backwards. The pubes and ischia are comparatively small. The femur is very long as compared with that of the Ungulata vera. There is no third trochanter. The fibula is complete. The foot is short and broad, somewhat smaller than the manus.

Skeleton of the Carnivora.—In the Carnivora the atlas is very large, with wing-like lateral processes. The neural spine of the axis is elongated and compressed, the odontoid conical. The other cervical vertebræ have small spines and large transverse processes. There are twenty or twenty-one thoracico-lumbar vertebræ. The most anterior thoracics have long, slender, backwardly-sloping spines. In the posterior thoracics large metapophyses and anapophyses are developed. The transverse processes of the lumbar vertebræ are extremely long and the spines short. The sternum is long and narrow, composed usually of eight or nine pieces. The sternal ribs are almost unossified.

In the *skull* of the Carnivora vera (Figs. 1097 and 1099) there are prominent sagittal and lambdoidal crests. The temporal fossæ are very deep; the orbits are not separated from them by bone. The relative development of the facial region varies in the different groups; in the Bears and their allies, and in the Dogs, it is elongated; in the Cats it is very short. The zygoma is strong and greatly arched outwards. The glenoid cavity is in the form of a transverse groove to the shape of which the transversely elongated condyle is adapted. In the Cats there is a large rounded tympanic bulla (Fig. 1098), the cavity of which is divided into two parts, anterior and posterior, by a septum, the anterior containing the auditory ossicles and the opening of the Eustachian tube; the bony auditory meatus is short: the paroccipital is closely applied to the posterior surface of the tympanic bulla. In the Dogs the septum of the bulla is incomplete, the auditory meatus short, and the paroccipital process not applied to the bulla. In the Bears and their allies (Fig. 1100), the bulla is usually less dilated, and the septum is absent or only represented by a ridge, while the bony auditory meatus is elongated.

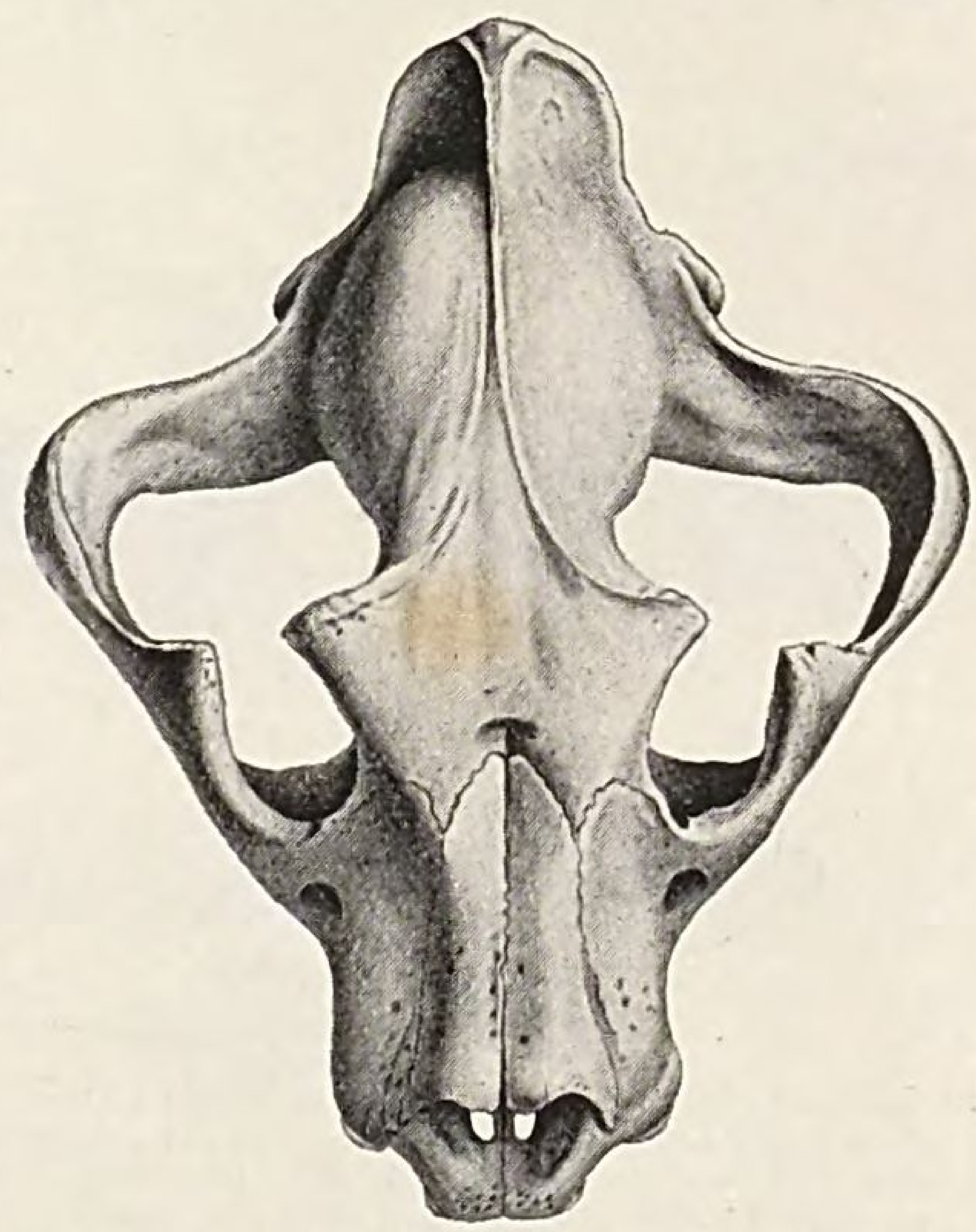


FIG. 1097.—Skull of **Tiger** (*Felis tigris*). (After Blainville.)

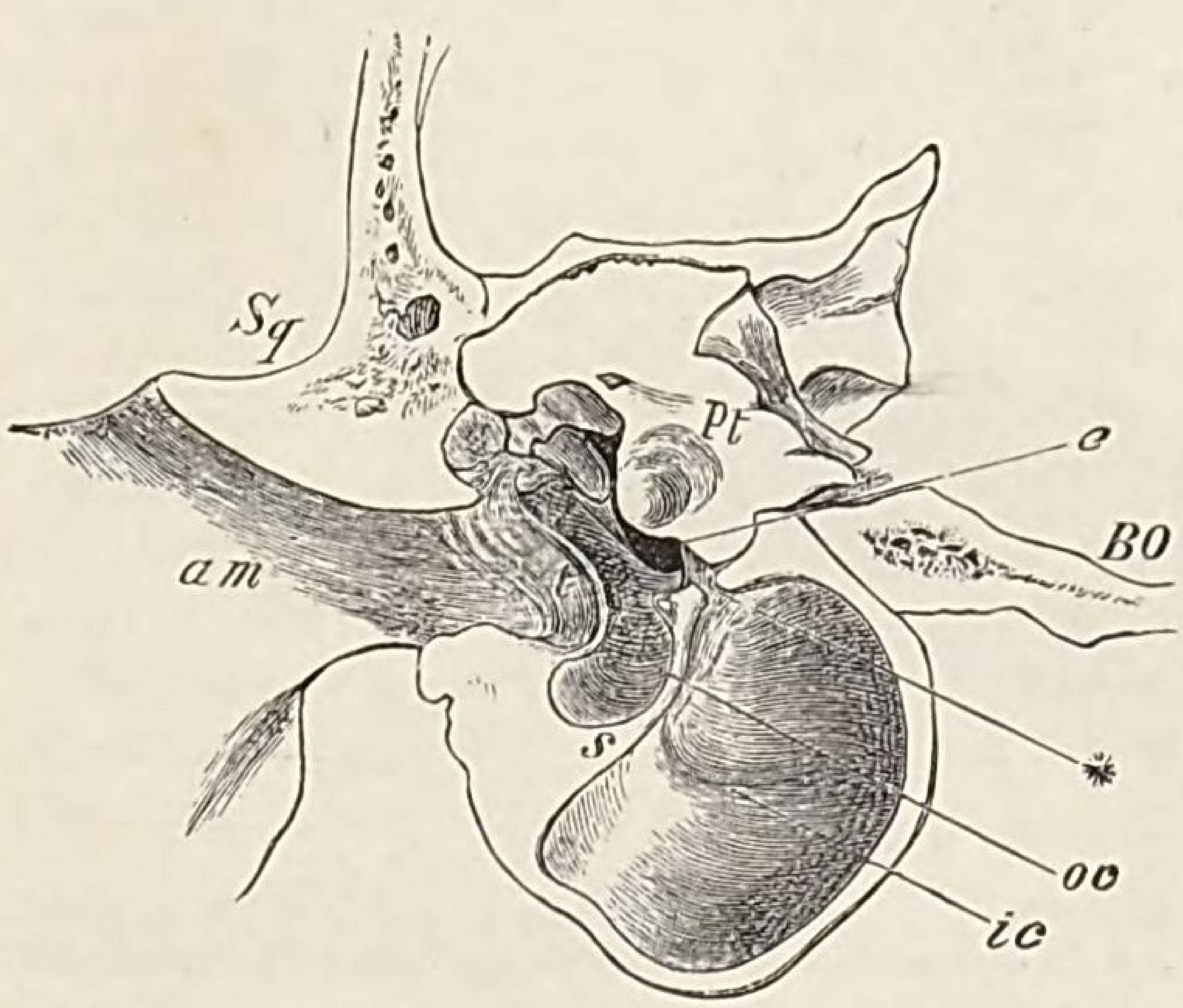


FIG. 1098.—Section of the left auditory bulla of **Tiger** (*Felis tigris*). *a.* aperture of communication between the two chambers into which the cavity of the bulla is divided; *a. m.* external auditory meatus; *b.oc.* basi-occipital; *Pt.* periotic; *s.* septum between the two chambers; *Sq.* squamosal. (After Flower.)

The cranium in the Pinnipedia is broad and rounded, rather compressed

from above downwards. The orbits are large and approach near to one another.

In the Carnivora vera the spine of the *scapula* is situated at

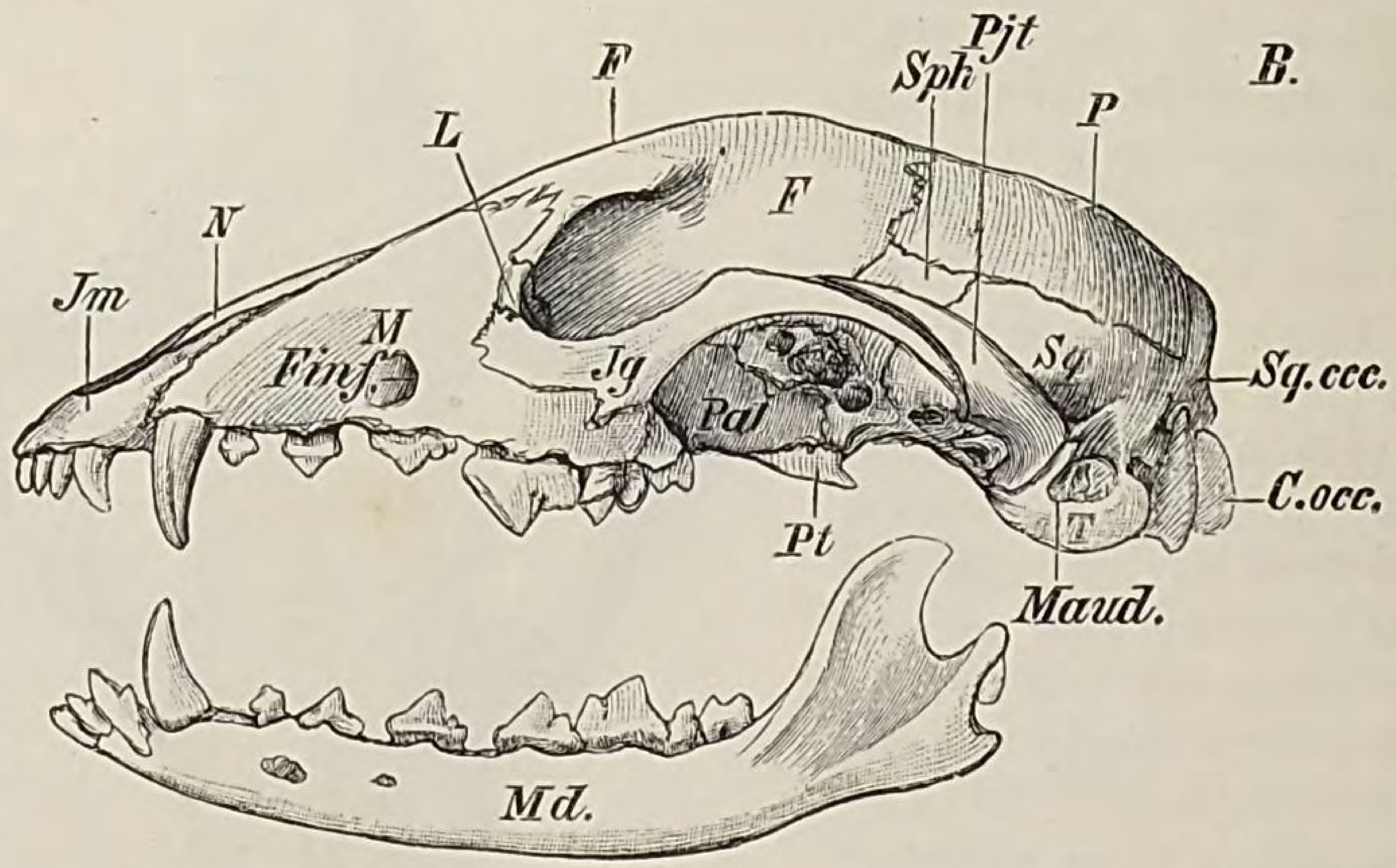


FIG. 1099.—Lateral view of skull of **Wolf** (*Canis lupus*). *C. occ.* occipital condyle; *F.* frontal; *F. inf.* infra-orbital foramen; *Jg.* jugal; *Jm.* pre-maxilla; *L.* lacrymal; *M.* maxilla; *M. aud.* external auditory meatus; *Md.* mandible; *N.* nasal; *P.* parietal; *Pal.* palatine; *Pt.* pterygoid; *Sph.* ali-sphenoid; *Sq.* squamosal; *Sq. occ.* supra-occipital; *T.* tympanic. (From Wiedersheim's *Comparative Anatomy*.)

about the middle of the outer surface of the bone. The acromion is usually well developed, sometimes with a metacromion. The coracoid is very small. The clavicle is never complete, some-

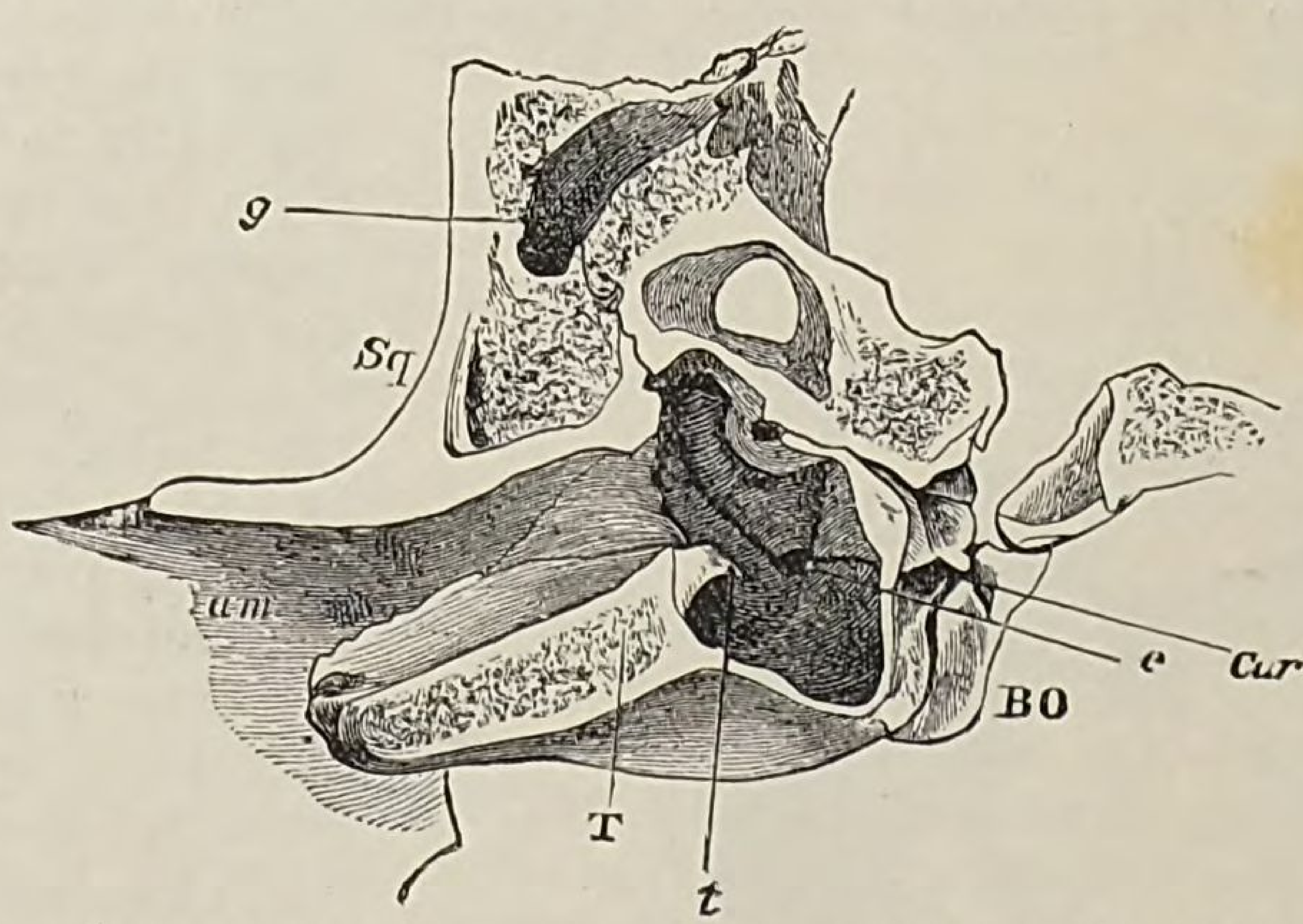


FIG. 1100.—Section of the left auditory bulla and surrounding bones of a **Bear** (*Ursus ferox*). *a. m.* external auditory meatus; *B.O.* basi-occipital; *e.* eustachian tube; *Sq.* squamosal; *T.* tympanic; *t.* tympanic ring. (After Flower.)

times entirely absent. There is a supra-condyloid foramen in the Cats and some of the other groups, not in the Dogs or Bears.

The scaphoid and lunar are united (Fig. 1101). There is no centrale. Usually a radial sesamoid is present. There are five digits, though the pollex may be reduced in size, as in the Dog and it is rudimentary in the Hyæna.

The *pelvis* is long and narrow. In the tarsus all the ordinary bones are developed. The hallux is fully formed in the Bears, etc.,

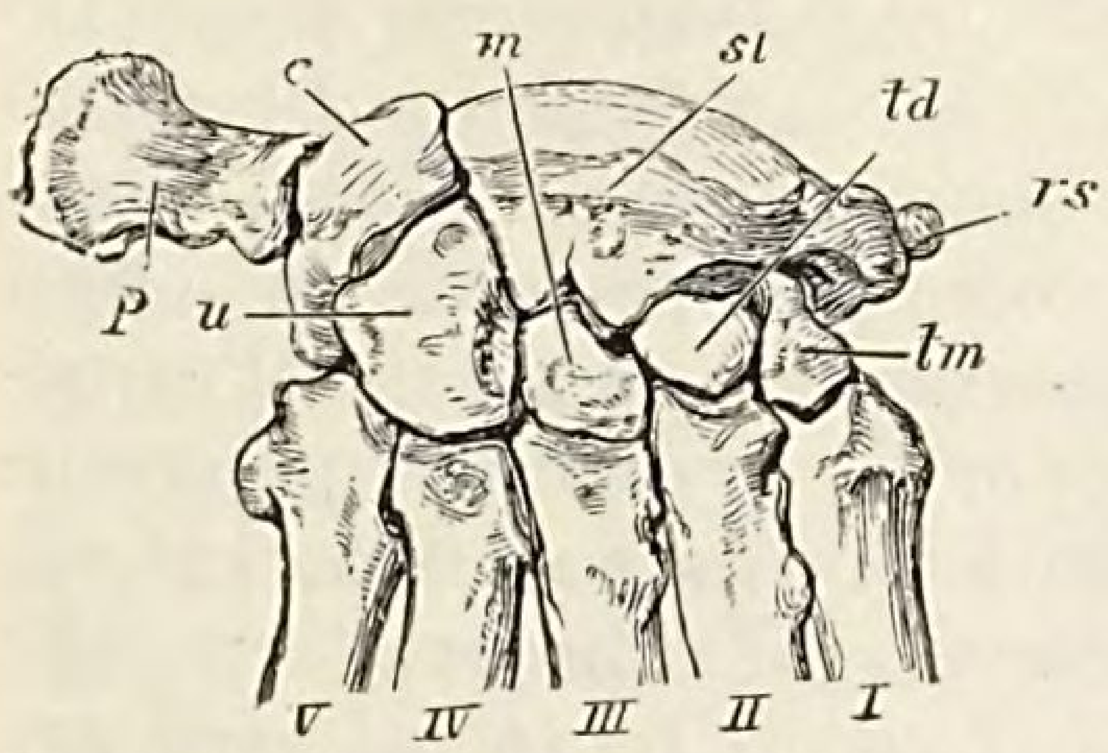


FIG. 1101.—Carpus of **Bear** (*Ursus americanus*). *c.* cuneiform ; *m.* magnum ; *p.* pisiform ; *r. s.* radial sesamoid ; *s. l.* scapho-lunar ; *td.* trapezoid ; *tm.* trapezium ; *u.* unciform. (After Flower.)

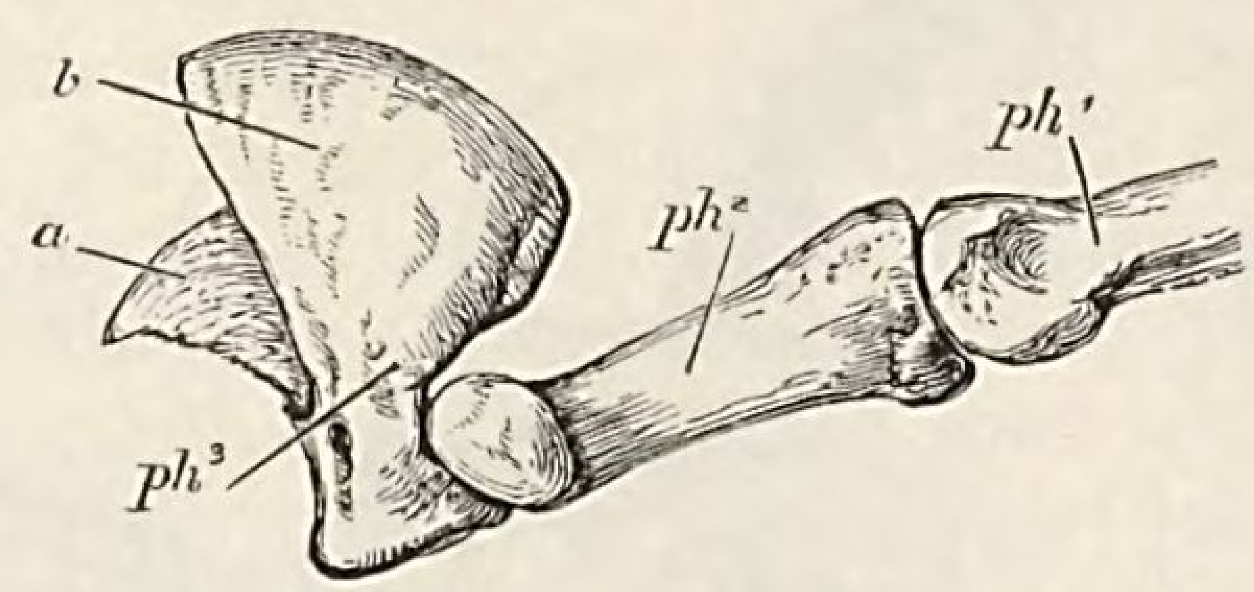


FIG. 1102.—The phalanges of the middle digit of the manus of the **Lion** (*Felis leo*). ph^1. proximal phalanx ; ph^2. middle phalanx ; ph^3. ungual phalanx ; *a*, the central portion forming the internal support to the horny claw ; *b*, the bony lamina reflected around the base of the claw. (After Flower.)

but shorter than the other digits. In the Cats and Dogs it is represented only by a rudiment of the metatarsal.

In the Pinnipedia (Fig. 1103) both acromion and coracoid are short, the scapula is curved backwards ; there is no clavicle. The bones of the fore-limb are short and stout ; the humerus has a prominent deltoid crest ; there is no foramen above the inner condyle. The ulna is greatly expanded at its proximal, the radius at its distal end. The manus is broad and expanded. The scaphoid and lunar are united to form a scapho-lunar. The ungual phalanges are nearly straight, slender and pointed. The ilia are short ; the symphysis pubis is short and without firm union of the bones. The femur is short, thick and flattened. The fibula and tibia are commonly ankylosed proximally. The calcaneum is short and usually without a distinct calcaneal process ; the lateral digits are usually the longest.

Skeleton of the Rodentia.—Among the Rodents the Jerboas are exceptional in having the cervical vertebræ ankylosed. Generally, as in the Rabbit, the transverse processes of the lumbar vertebræ are elongated. As in the Ungulata the sacrum usually consists of one broad anterior vertebra followed by several narrower ones. The caudal region varies in length in the different families ; in most it is very short, but it is elongated in some (the Porcupines, Squirrels and Beavers). The sternum of the Rodents has a long and narrow body ; sometimes there is a broad pre-sternum ; the posterior end is always expanded into a cartilaginous xiphisternum.

The *skull* is elongated, narrow in front, broader and depressed

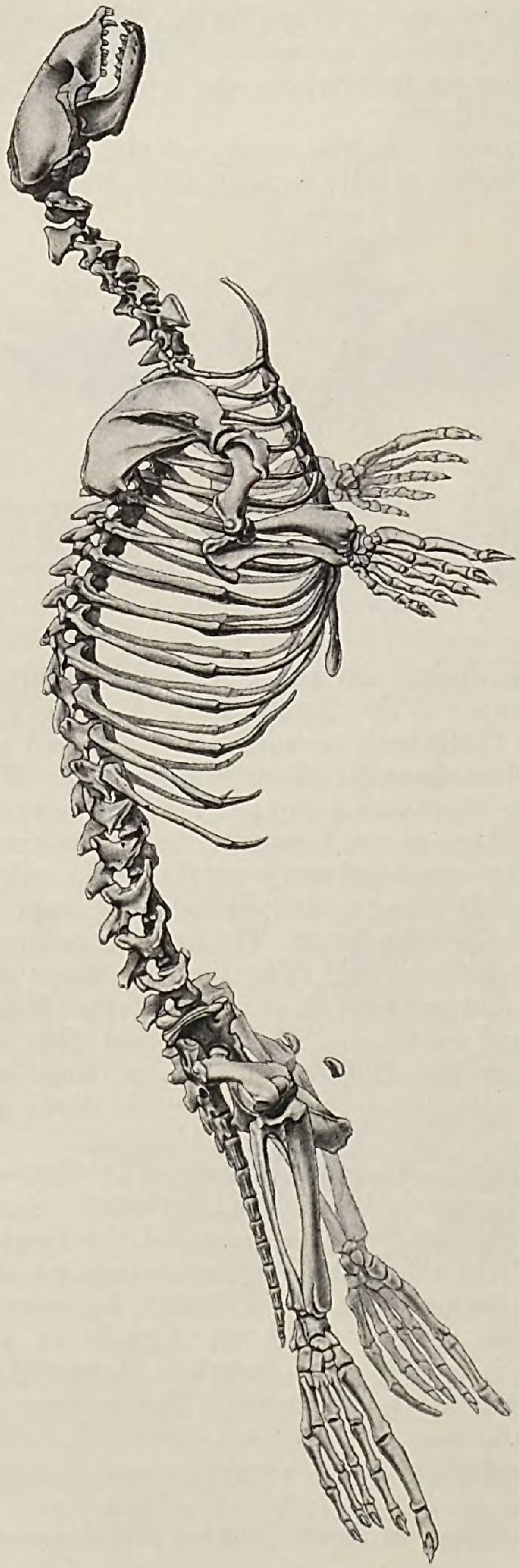


Fig. 1103.—Skeleton of **Seal** (*Phoca vitulina*). (After Blainville.)

behind. The nasal cavities are very large, especially in the Porcupines, with air sinuses in the upper part. In some the optic foramina fuse into one. An inter-parietal is often present. Par-oc-cipital processes are developed. The orbit and the temporal fossa are always continuous. The nasal bones are large, and the nasal apertures are terminal or nearly so. The pre-max-illæ are always very large. A re-markable feature of the skull is the presence in many of a large open-ing corresponding to the infra-orbital foramen. The middle part of the zygoma is formed by the jugal; the latter often helps to bound the glenoid cavity as in the Marsupials. The palate is short, and the anterior palatine foramina large. The peri-otic and tympanic are ankylosed to-gether, but not to the neighbouring bones. The coro-noid process of the

mandible is sometimes rudimentary or absent; the angle is often produced into a process.

The scapula of the Rodentia is generally long and narrow. The spine sometimes has a metacromion process and a long acromion. The coracoid process is small. The clavicle varies as regards its development. Vestiges of the sternal end of the coracoid are sometimes distinguishable. There is considerable variation in the bones of the arm and fore-arm. The radius and ulna are in most instances distinct, though in close and firm apposition. The scaphoid and lunar are usually united; the centrale is sometimes present, sometimes absent. The pelvis and femur vary greatly. Sometimes there is a third trochanter. The fibula is sometimes distinct, sometimes fused with the tibia. In the Jerboa the metatarsals of the three digits are fused together.

Skeleton of the Insectivora.—The neural spine of the axis is usually well developed, that of the remaining cervical vertebræ small or obsolete. The number of trunk vertebræ varies in the different families from eighteen to twenty-four, and there is also great variation in the development of the various processes. The caudal region varies in its length; frequently it has chevron bones. The presternum is expanded, the mesosternum composed of distinct narrow sternebræ.

The *skull* (Fig. 1104) varies greatly in the different families, in the higher forms approaching that of the Lemurs, with com-

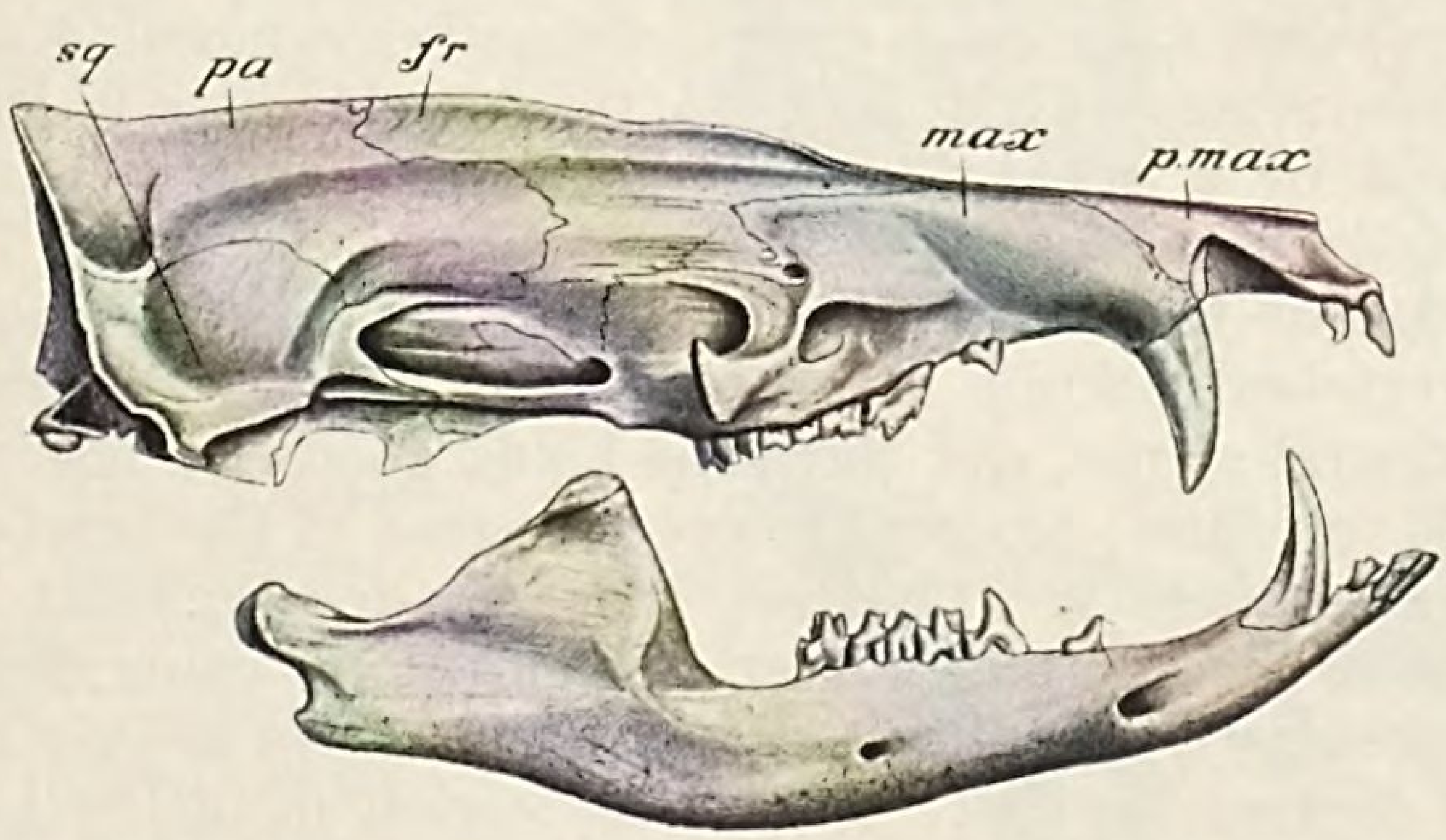


FIG. 1104.—Skull of **Tenrec** (*Centetes ecaudatus*). *fr*. frontal; *max*. maxilla; *pa*. parietal; *p.max*. pre-maxilla; *sq*. squamosal. (After Dobson.)

paratively large cerebral fossæ, large orbits with complete or nearly complete bony rims, well developed zygoma, and a tympanic bulla and tubular auditory meatus. In the others the cranial capacity is less, and the orbits and temporal fossæ are completely continuous; the zygoma is incomplete, and the tympanic does not usually form a bulla.

The *pectoral arch* also varies a good deal in the different families of the Insectivora. In the true Moles and their allies there is a remarkable bone of cuboid shape articulating ventrally with the presternum and dorsally with the humerus, and only connected by a ligamentous band with the scapula. Its mode of formation from a mass of cartilage to the anterior face of which the clavicle, formed as usual in membrane, becomes applied, proves that this bone represents a pro-coracoid as well as a clavicle. In the rest this bone is not developed, and the clavicle is a distinct, long and slender bone, but vestiges of the inner or ventral ends of the coracoid and pro-coracoid may be recognisable. Sometimes the "mesoscapular segment" is represented by a distinct bone intervening between the outer end of the clavicle proper and the acromion process.

The humerus usually has a supracondylar foramen. In the Moles this is absent, and the humerus is remarkable in other respects, being short, greatly expanded at the extremities, with a prominent deltoid ridge, and with two synovial articular surfaces at the proximal end, one for the glenoid cavity of the scapula, the other for the coraco-clavicle. The radius and ulna are completely developed and usually distinct, but are sometimes fused distally. In the carpus the scaphoid and lunar sometimes coalesce, sometimes remain distinct; an os centrale is usually present. In the Moles the manus is extremely broad, the breadth being increased by the presence of a large curved radial sesamoid.

In the *pelvis* the symphysis pubis is sometimes elongated, sometimes short, sometimes absent, the pubes remaining separated by a wide median ventral cleft. A third trochanter is sometimes represented by a ridge. The fibula usually, though not always, fuses distally with the tibia.

Skeleton of the Chiroptera (Fig. 1105).—The cervical region of the vertebral column is characterised by the absence of any distinct neural spines, and the same holds good to a less extent of the trunk vertebræ; the transverse processes of the lumbar region are also rudimentary. The tail varies in development: when it is elongated the component vertebræ are long cylindrical centra without processes. Sagittal and occipital crests are developed in the skull of some species. The facial region is rather elongated, especially in the Megachiroptera (Fig. 1106). The post-orbital processes of the frontal are present or absent: the zygoma is long and slender: the malar is small and applied to the outer surface of the zygoma. The long and narrow nasals are sometimes united; the pre-maxillæ are small. The mandible has an angular process in the Microchiroptera, not in the Megachiroptera. The segments of the sternum are sometimes distinct, sometimes united, the presternum has a mesial keel developed in co-ordination with the great size of the pectoral muscles. The sternal ribs are ossified.

The *scapula* is large and oval in shape: the spine is near the anterior margin: the post-scapular fossa has ridges for the origin of the muscular fibres: the spine has a well developed acromion. The coracoid process is elongated and in some cases bifurcated. The clavicle is long. The pro-coracoid is represented by a separate ossification; there are rudiments of the sternal end of the coracoid between the clavicle and the first rib. The humerus, radius and ulna are all elongated. The ulna is reduced, and is sometimes only represented by the proximal end, ankylosed with the radius. A large sesamoid is developed in the tendon of the triceps muscle near the olecranon process of the ulna. In the carpus the scaphoid and lunar are united: sometimes also the cuneiform is united with these: the pisiform is small. There is no centrale. The ungual phalanges are absent in the nail-less digits. The pelvis is small, the symphysis pubis often imperfect. The fibula is some-

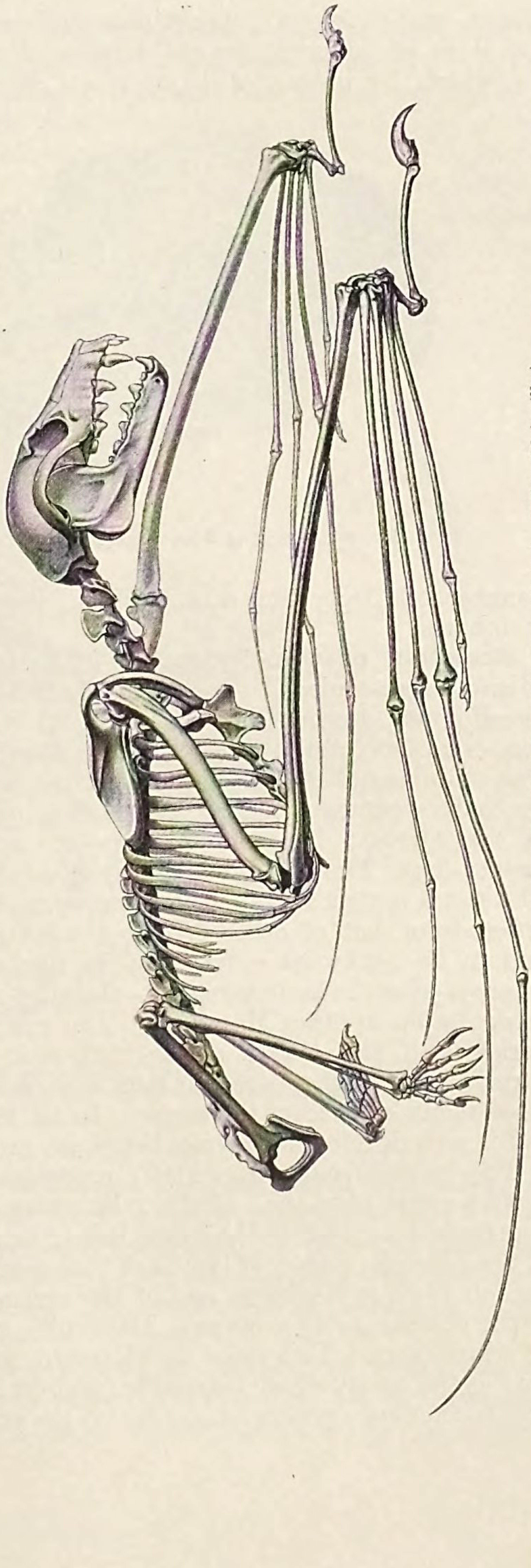


FIG. 1105.—Skeleton of **Flying Fox** (*Pteropus jubatus*) (After Blainville.)

times well-developed, sometimes rudimentary. The tuber calcanei is an inwardly curved process of the calcaneum, attached to which by means of ligamentous fibres is a slender rod of

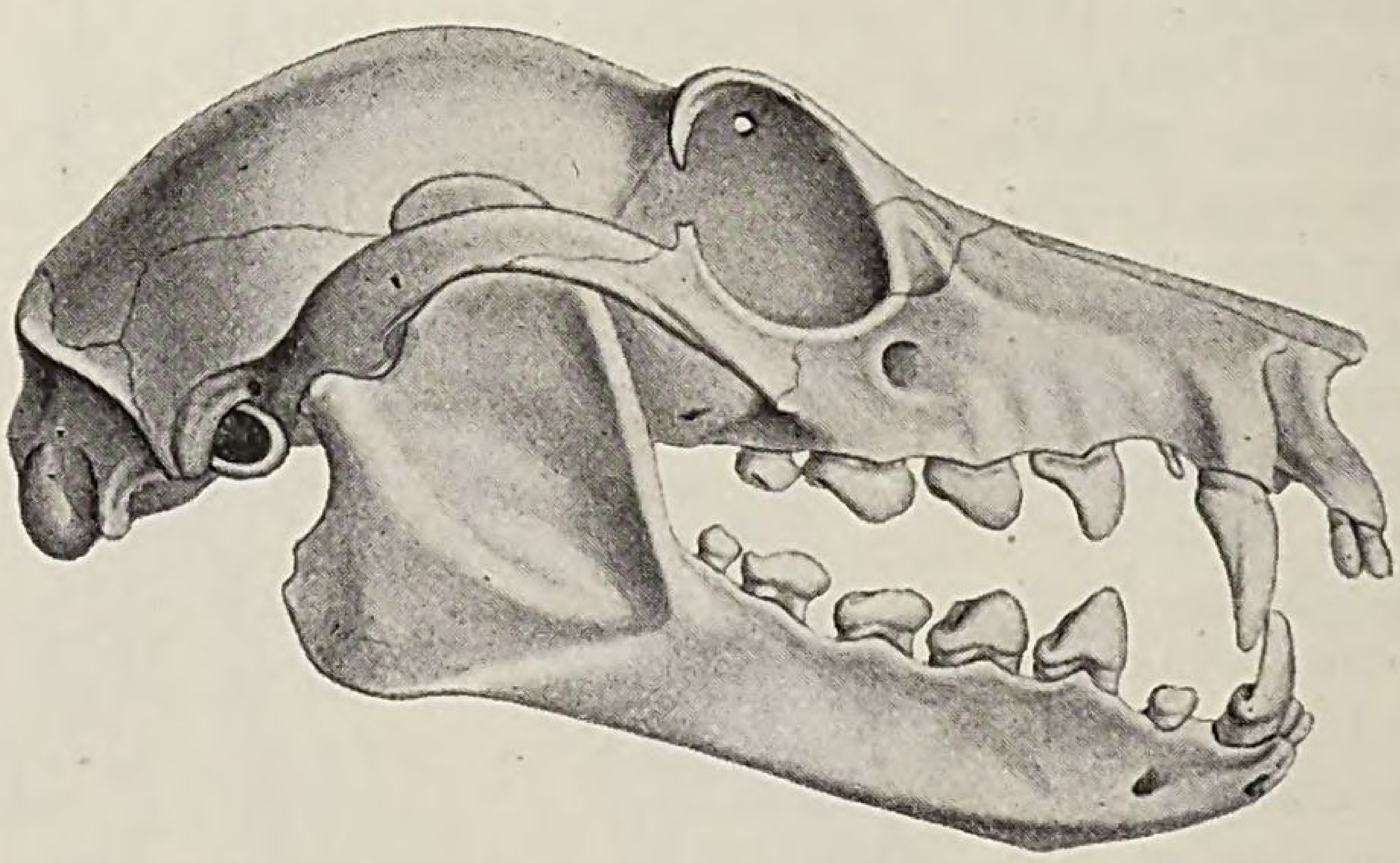


FIG. 1106.—Skull of **Pteropus fuscus.** (After Blainville.)

bone or cartilage, the *calcar*, which supports the inter-femoral membrane.

Skeleton of the Primates.—The atlas is ring-like, the odontoid sub-conical. The spines of the cervical vertebræ are usually well developed and simple: in Man they are short, with the exception of the seventh, and bifid: in some they are trifid. The number of thoracico-lumbar vertebræ is usually nineteen, but only seventeen in Man, the Gorilla and Chimpanzee, sixteen in the Orang; in some Lemurs it may be twenty-three or twenty-four. The number of sacral vertebræ varies from two to five. The sacral region of Man, which comprises five ankylosed vertebræ, differs from that of other Primates in its greater relative breadth and in its backward curvature; it forms a well-marked angle where it joins the lumbar region—the *sacro-vertebral angle*—scarcely recognisable in other Mammals. The number of caudal vertebræ varies with the length of the tail, from four to about thirty-three. In Man there are only four vestigial caudal vertebræ, ankylosed together to form the *coccyx*. In all those forms in which the tail is well developed chevron bones are present.

The human *skull* (Fig. 1107) presents a marked contrast in certain respects to that of other Mammals, but in many points is approached by that of the other Primates, more especially by that of the Simiidæ. One of the most important characteristics of the human skull is the large size of the brain-case, the cubic content of the cranial cavity averaging 1500 cubic centimetres in the male of white races. This great development is most marked in that part of the cavity which lodges the cerebral hemispheres, in adaptation to the large dimensions of which the cranium bulges out both

anteriorly and posteriorly to such an extent that the entire length of the cavity greatly exceeds that of the basi-cranial axis. A result of the posterior bulging of the brain-case is that the foramen magnum (*f.m*) is no longer situated at the posterior extremity of the skull as in other Mammals, but assumes a position further forwards towards the middle of the base. The anterior expansion, causing a strong arching forwards of the frontal region, brings about an alteration in the position of the ethmoidal plane, which, instead of

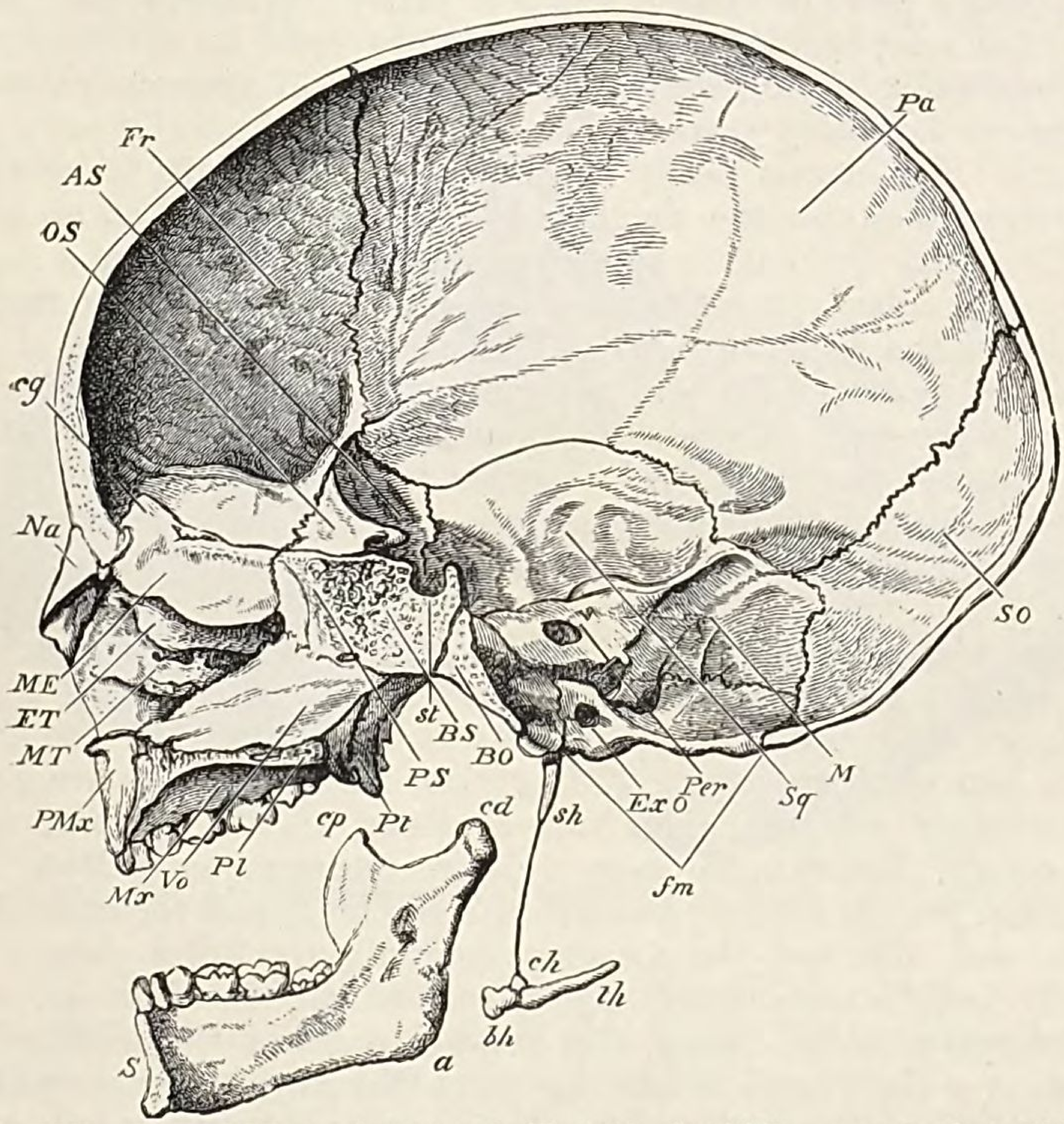


FIG. 1107.—Skull of **Man.** Letters as in Fig. 1086. In addition, *a.* angle of mandible; *c.g.* crista galli, a process of the mesethmoid; *s.t.* sella turcica. (After Flower.)

being perpendicular or inclined to the basi-cranial axis, becomes horizontal, and the cribriform plate forms the middle part of the floor of the anterior extension of the cranial cavity. The fossa for lodgment of the cerebellum lies entirely beneath the posterior portion of the cerebral fossa: the olfactory fossa is comparatively small. (See Fig. 1057, *D.*)

The outer surface is smooth and rounded, devoid of any prominent ridges or crests. The occipital crest of lower Mammals is represented merely by a rough raised line—the *superior curved*

line of the occiput. The par-occipital processes are only represented by slight eminences—the *jugular eminences.* There is no auditory bulla; the mastoid portion of the periotic projects downwards as a prominent *mastoid process.* The periotic, tympanic, and squamosal early fuse into one bone—the *temporal bone.* The post-glenoid process is very slightly developed. The whole facial region is relatively small. The orbits, which are of moderate size, are directed forwards; the bony margin is complete, and a plate of bone developed partly from the jugal, partly from the alisphenoid, almost completely cuts it off from the temporal fossa, leaving only a small aperture of communication—the *spheno-maxillary fissure.* The frontal suture usually early disappears. The nasals rarely become fused. The suture between the premaxillæ and the maxillæ becomes obliterated at an early stage, so that the entire upper jaw appears to consist of a single bone. A peculiar spine, the *nasal spine,* is developed in the middle line below the nasal opening. The most marked feature of the mandible is the presence of a prominence, the *mental prominence,* in the lower part of the symphysial region (*S.*). The stylo-hyal nearly always becomes fused, together with the tympano-hyal, to the periotic and tympanic, giving rise to a slender process—the *styloid process* (*sh.*)—projecting downwards from the base of the skull.

None of the other Primates have a cranial capacity approaching that of Man; and those modifications in the shape of the skull, which are the concomitants of the great development of the brain in the human species, are accordingly not recognisable, or are much less strongly marked. The various fossæ of the cranium, as a rule, occupy, however, the same relative positions as in Man; the cerebellar fossa is entirely beneath the cerebral; and the ethmoidal plane, and that and the foramen magnum (occipital plane) are usually both horizontal or nearly so. In all the Simiidæ, with the exception of the Orang, the frontals meet in the middle line below, over the presphenoid. In many Monkeys the outer surface of the cranium is smooth and free from prominent ridges; but in the Baboons, the Orangs, the Gorilla, and the Chimpanzee (Fig. 1108), there are strongly developed occipital, sagittal, and supra-orbital ridges, usually much more prominent in the male than in the female, and increasing in size with age. The par-occipital processes are always rudimentary, but there are well-marked post-glenoid processes. The mastoid does not form a distinct mastoid process. In the Cebidæ and Hapalidæ alone is there a tympanic bulla. The entire facial region is relatively larger than in Man; the premaxillo-maxillary region is always more prominent, and in the Baboons projects forwards as a distinct muzzle. The orbit is separated from the temporal fossa as in Man. The nasals are usually ankylosed in the adult. The nasal spine is never developed. The

suture between the premaxilla and the maxilla only becomes obliterated, if at all, in old individuals. The mental prominence of the mandible is never developed, the anterior surface of the symphysial region sloping backwards and downwards from the bases of the incisor teeth. The stylo-hyal never gives rise to an ossified styloid process.

In the skull, as in many other respects, the Lemurs occupy an intermediate position between the higher Primates and the lower orders of Mammals. The occipital and ethmoidal planes are usually vertical. The tympanic forms a large bulla. The orbits, which are large, are usually separated from the temporal fossa

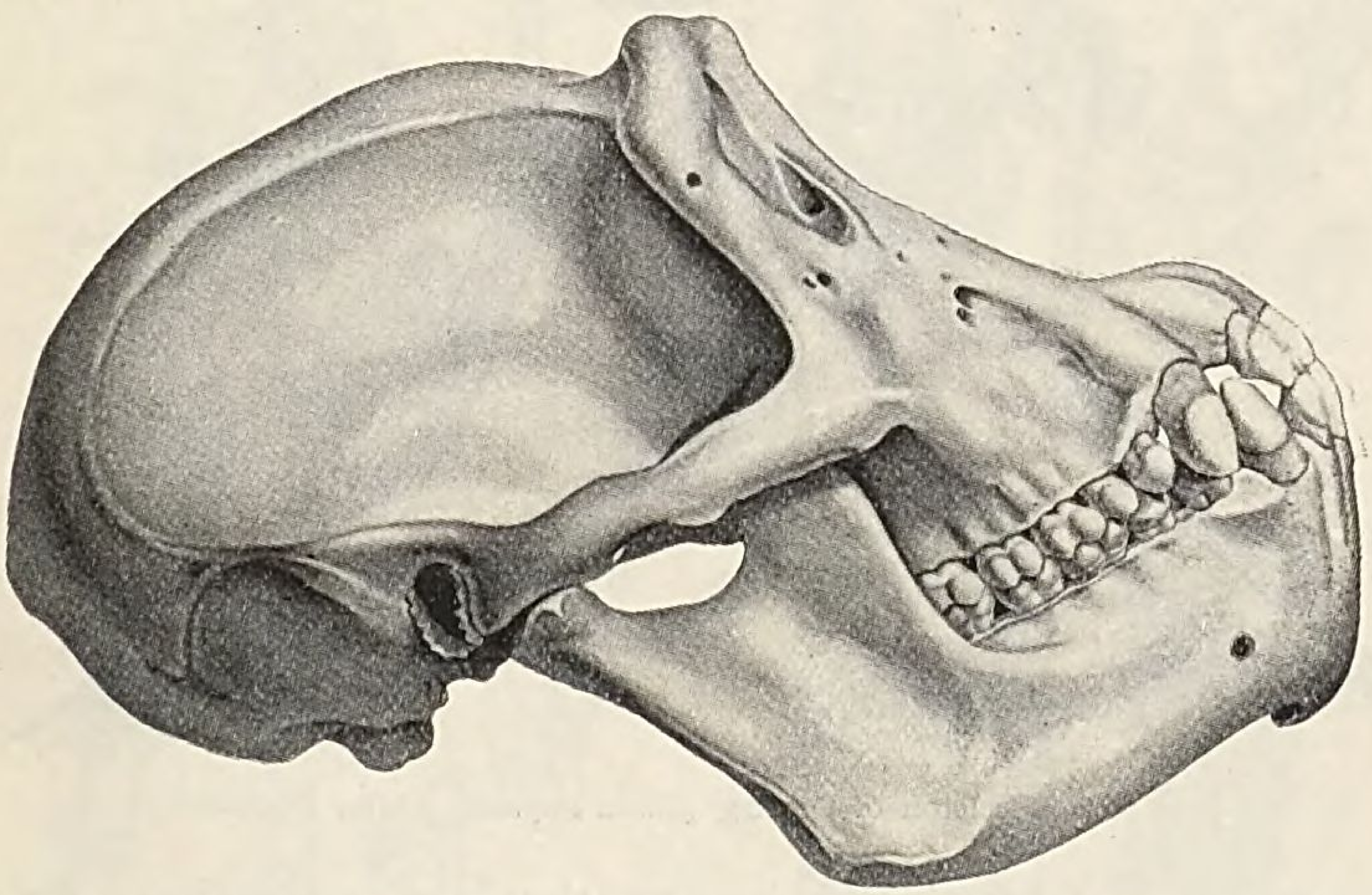


FIG. 1108.—Skull of **Chimpanzee** (*Anthropopithecus troglodytes*). (After Blainville.

only by a narrow rim of bone. The lacrymal foramen is situated on the face outside the margin of the orbit. The facial region is usually elongated, and may form a prominent muzzle.

In all the Primates the clavicle is present and complete, and in the scapula, the spine, acromion, and coracoid process are well developed. In Man and the higher Apes the glenoid border of the scapula is much longer than the coracoid. In the lower Monkeys, on the other hand, these borders are nearly equal. The humerus is comparatively long and slender; the tuberosities and ridges are not, as a rule, very strongly developed. In Man and the Simiidæ the bone is twisted around its long axis; in the lower forms this torsion is absent. In Man and the higher Apes the foramen above the inner condyle is absent; it is present in many of the American Monkeys and in most Lemurs. Characteristic of the ulna of Man and the higher Apes is the small upward extension of the olecranon process. The radius and ulna are distinct in all

in the higher forms the shafts of the two bones are bent outwards, so that there is a wide interosseous space, and there is consider-

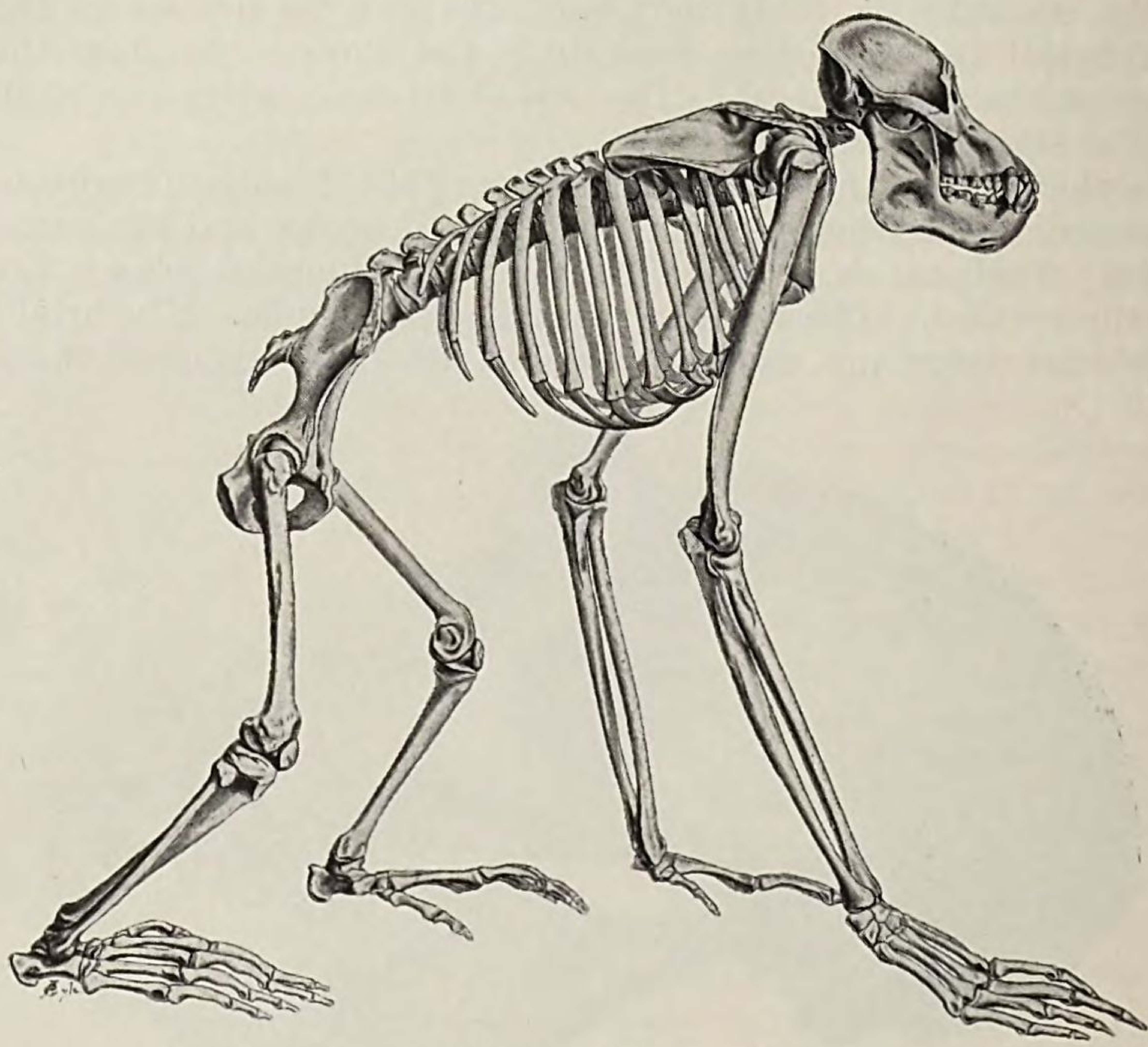


FIG. 1109.—Skeleton of **Orang** (*Simia satyrus*) (After Blainville.)

able freedom of movement in pronation and supination. In the carpus (Fig. 1110) the scaphoid and lunar are always distinct, and a centrale is present in all except some of the Lemurs, the Gorilla, Chimpanzee, and Man. A pisiform is present, and in most a radial sesamoid. As compared with that of the other Primates, the carpus of Man is short and broad; the trapezium has a saddle-shaped articular surface turned somewhat inwards. In Man, the Chimpanzee, Gorilla, and Orang, the carpus articulates exclusively with the radius; in all the others it articulates also with the ulna. In Man the pollex has a remarkable and characteristic freedom of movement in opposition to the other digits.

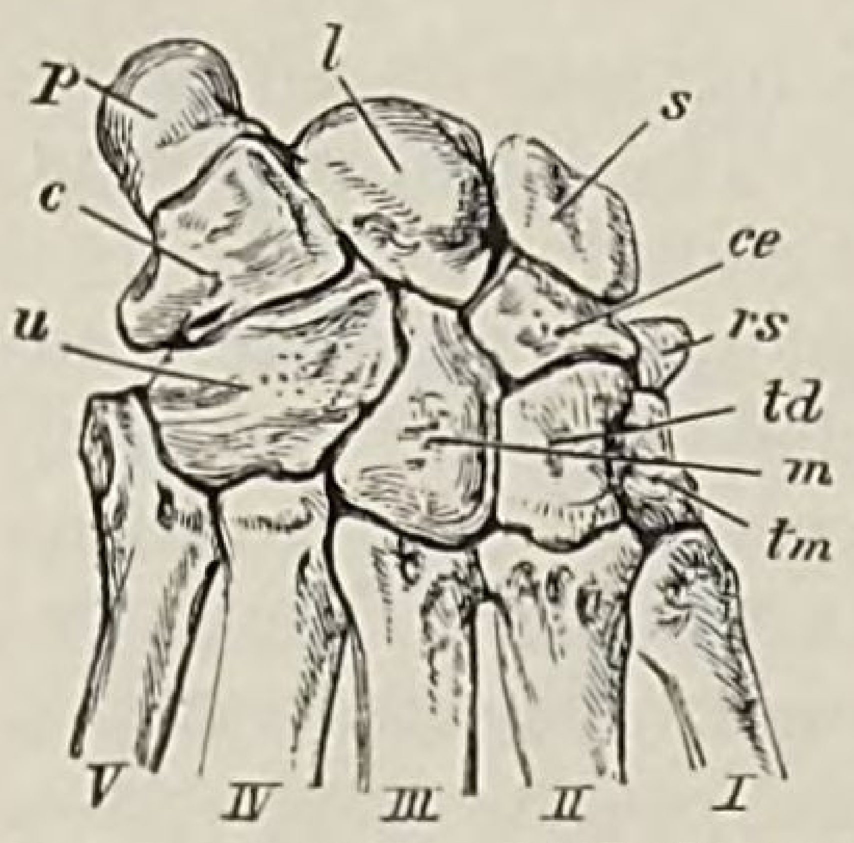


FIG. 1110.—Carpus of **Baboon** (*Cynocephalus anubis*). *ce.* centrale; *c.* cuneiform; *l.* lunare; *m.* magnum; *p.* pisiform; *r. s.* radial sesamoid; *s.* scaphoid; *td.* trapezoid; *tm.* trapezium; *u.* unciform. (After Flower.)

The human *pelvis* is remarkable for its relative breadth, for the expanded form of the ilia, and the deep concavity of their

inner surfaces, and for the shortness of the pubic symphysis. In the higher Apes some of these features are recognisable, though less pronounced; but in the lower the ilia are long and narrow, and usually curved outwards; in the Old-world Monkeys the tuberosities of the ischia are strongly everted and roughened for the attachment of the ischial callosities.

The tibia and fibula are well-developed and distinct in all. In nearly all the hallux, owing to the form and direction of the articulation between it and the internal cuneiform, is opposable to the other digits, converting the foot into a grasping organ. The

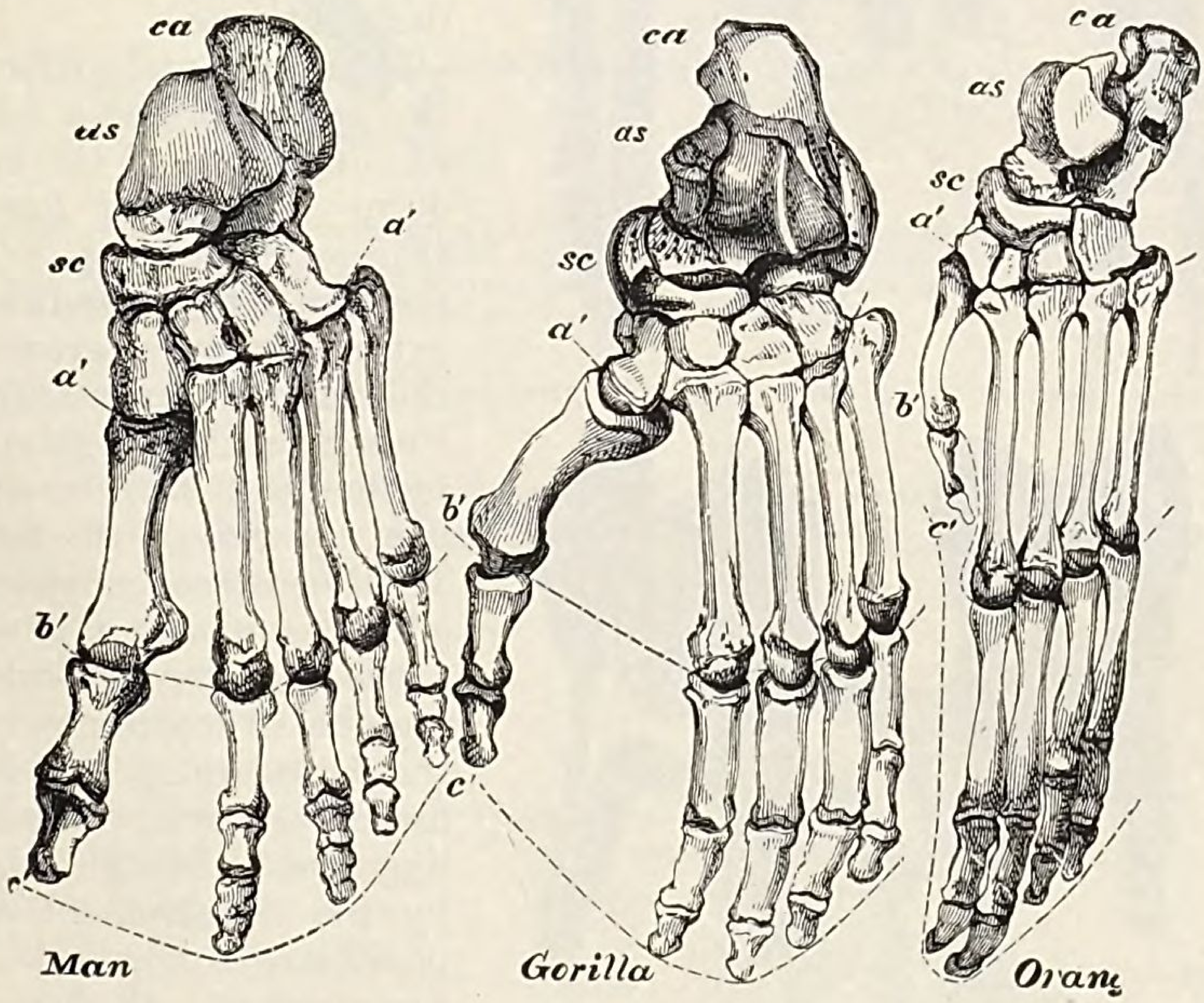


FIG. 1111.—Foot of **Man, Gorilla** and **Orang** of the same absolute length, to show the difference in proportions. The line *a' a'* indicates the boundary between tarsus and meta tarsus; *b' b'*, that between the latter and the proximal phalanges; and *c' c'* bounds the ends of the distal phalanges. *as.* astragalus; *ca.* calcaneum; *sc.* scaphoid. (After Huxley.)

human foot (Fig. 1111) is distinguished from that of the other Primates by the absence of this power of opposition, and by the relative length of the tarsus, which exceeds that of the metatarsus.

Digestive Organs.—*Teeth* are present in nearly all Mammals, but in some they are wanting in the adult condition (Whale-bone Whales and Platypus). In Echidna teeth are not present even in the young. In some of the Anteaters teeth are developed in the fœtus and are thrown off *in utero*—the adult animal being devoid of them.

Teeth, as already explained in the general account of the Craniata (p. 80), are developed in the epidermis and partly from the underlying dermis. In the Mammals each tooth is lodged in a socket or alveolus in the jaw. The part of the tooth developed from the epidermis is the enamel; the remainder of the tooth—dentine, cement and pulp—being formed from the subjacent mesodermal tissue.

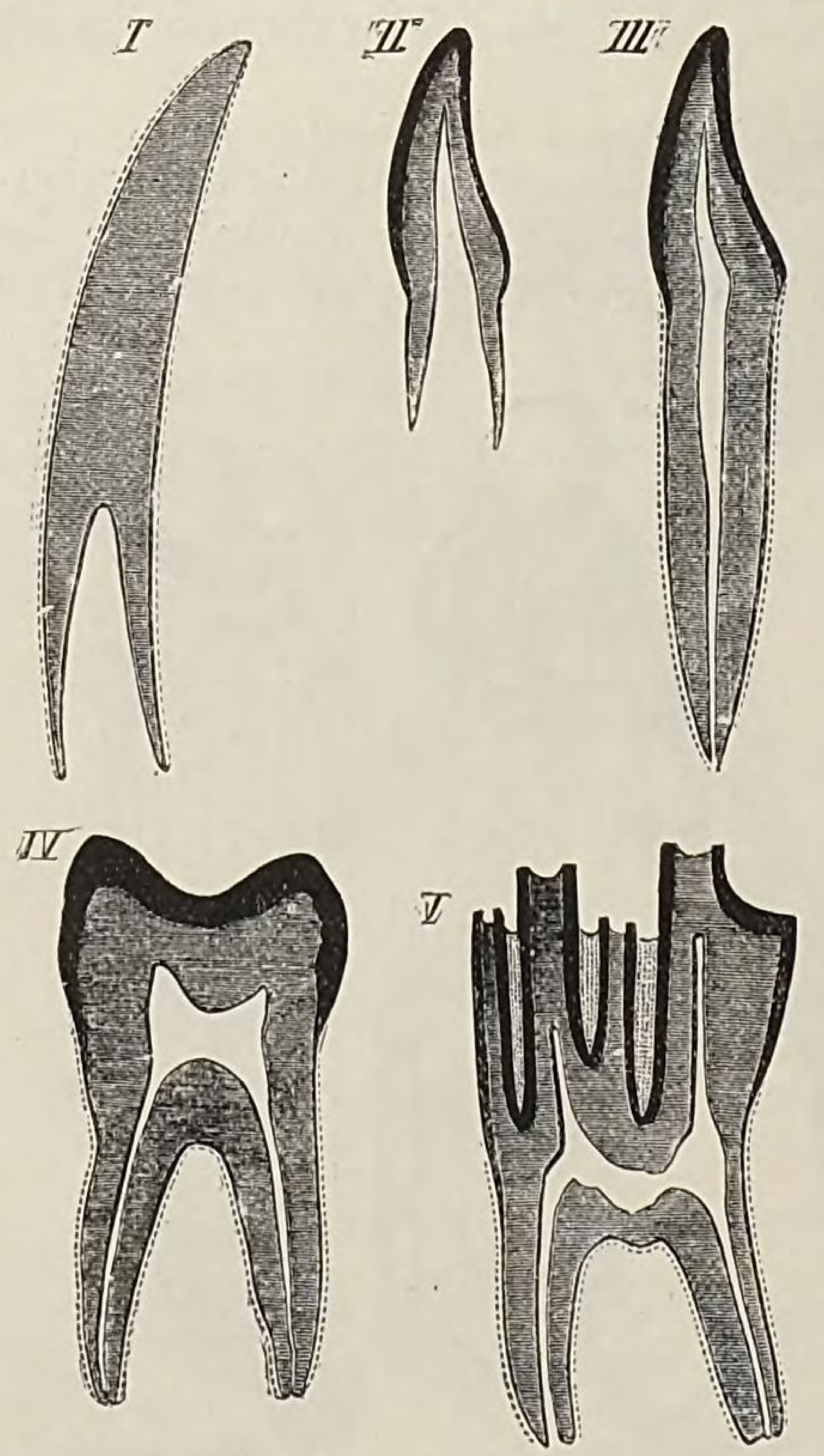


FIG. 1112.—Diagrammatic sections of various forms of teeth. I, incisor or tusk of Elephant with pulp cavity persistently open at base; II, human incisor during development, with root imperfectly formed, and pulp-cavity widely open at base; III, completely formed human incisor, with pulp cavity opening by a contracted aperture at base of root; IV, human molar with broad crown and two roots; V, molar of the Ox, with the enamel covering the crown deeply folded, and the depressions filled up with cement; the surface is worn by use, otherwise the enamel coating would be continuous at the top of the ridges. In all the figures the enamel is black, the pulp white; the dentine represented by horizontal lines and the cement by dots. (After Flower and Lydekker.)

Along the oral surface of the jaw is formed a ridge-like ingrowth of the ectoderm—the *dental lamina* (Fig. 1113, *lam.*). The position of this is indicated externally by a groove—the *dental groove* (*gr.*). From this a bud is given off in the position to be occupied by each of the teeth. This becomes constricted off as a conical cap of cells —the *enamel organ*—which remains in continuity with the dental ridge only by a narrow isthmus. This cap-like form is brought about by the development of a papilla of condensed dermal tissue, the *dental papilla* (*pap.*), which pushes upwards against the enamel organ. On the surface of this papilla, in contact with the enamel organ, the cells (*odontoblasts*) become arranged into a layer having the appearance of an epithelium—the *dentine forming layer*. The cells of the enamel organ form two layers, of which that in contact with the dental papilla assumes the character of a layer of long cylindrical cells—the *enamel membrane* (*en. m.*). The more superficial layer consists of cubical cells. Between the two the remaining

cells of the enamel organ become modified to form a kind of connective tissue—the *enamel pulp* (*en. plp.*).

The connective tissue immediately surrounding the entire rudiment of the tooth becomes vascular and forms a distinct

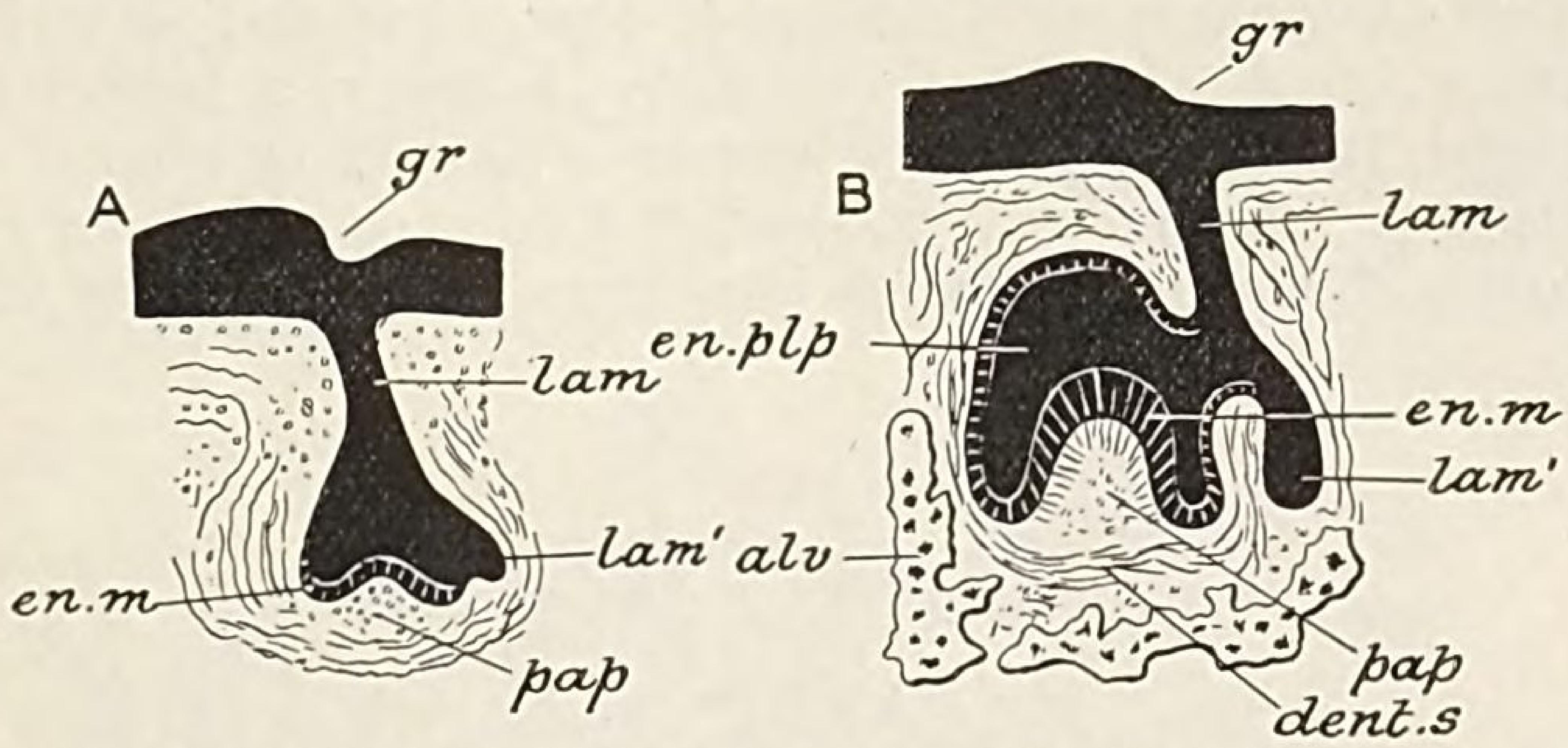


FIG. 1113.—Two stages in the development of the teeth of a **Mammal** (diagrammatic sections). *alv.* bone of alveolus; *dent. s.* dental sac; *en. m.* enamel membrane; *en. plp.* enamel pulp; *gr.* dental groove; *lam.* dental lamina; *lam'.* part of dental lamina which grows downwards below the tooth-germ; *pap.* dental papilla. (After O. Hertwig.)

investment—the *dental sac* (*dent. s.*); from this blood-vessels extend into the papilla.

Ossification begins by the formation of a cap of dentine (Fig. 1114, *dent.*) produced by the dentine-forming cells, and of a layer of enamel (*en.*) on the surface of this produced by the cells of the enamel-membrane. To these additional layers are added until the crown of the tooth becomes fully developed. The substance of the dental papilla gives rise to the pulp. As the tooth elongates it projects on the surface and eventually breaks through the mucous membrane of the gum, the remains of the enamel organ becoming thrown off. The cement is formed by the ossification of the connective tissue surrounding the tooth-papilla.

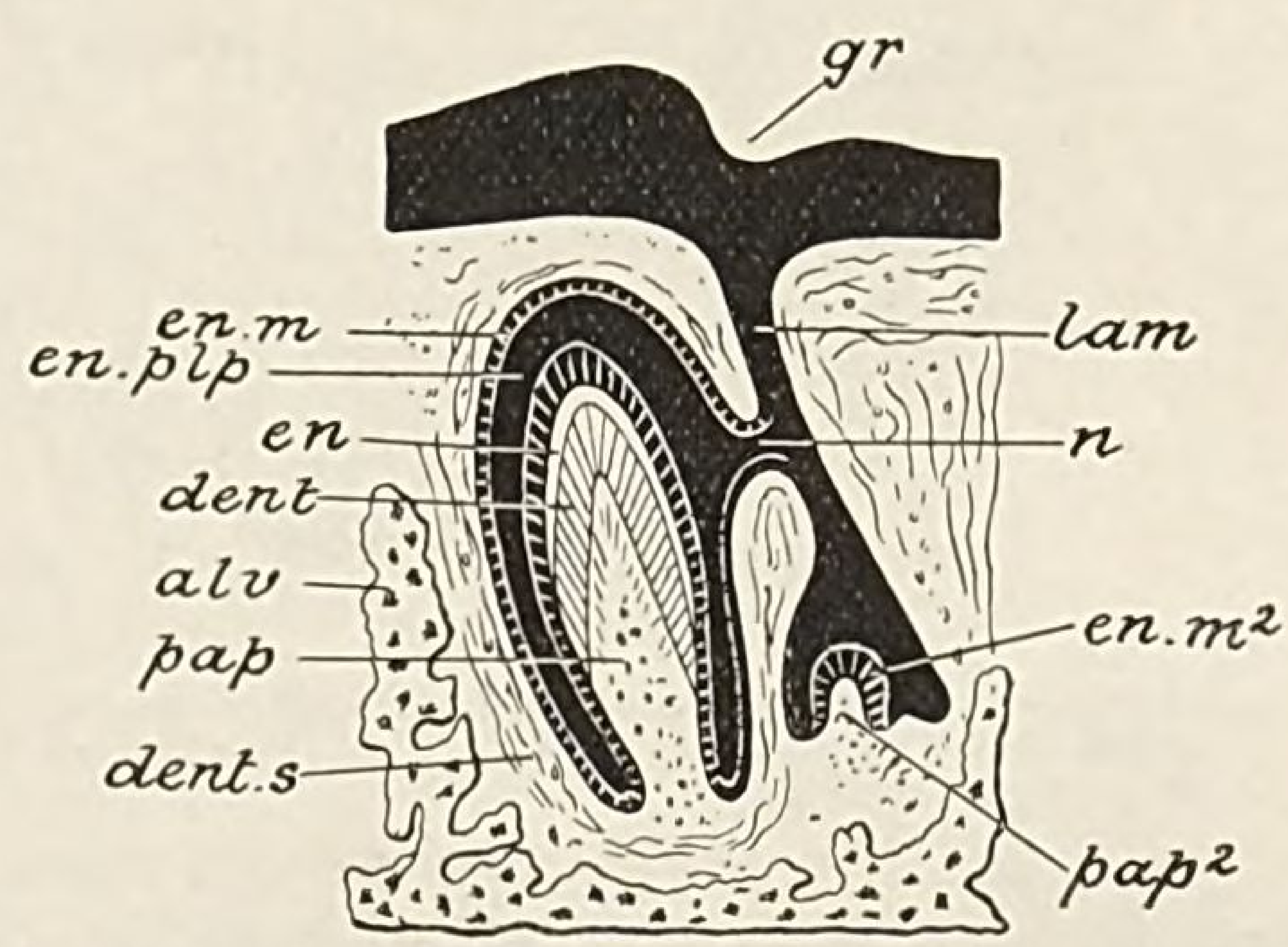


FIG. 1114.—Diagrammatic section showing the development of the milk and permanent teeth of **Mammals**. *alv.* bone of alveolus; *dent.* dentine; *dent. s.* dental sac; *en.* layer of enamel; *en. m.* enamel membrane of milk tooth; *en. m²*. enamel membrane of permanent tooth; *en. plp.* enamel pulp of milk tooth; *gr.* dental groove; *lam.* dental lamina; *n.* neck connecting milk tooth with lamina; *pap.* dental papilla of milk tooth; *pap²*. dental papilla of permanent tooth. (After O. Hertwig.)

In the teeth of most Mammals distinct *roots* are formed, each with a minute opening leading into the pulp-cavity (Fig. 1112, *III–V*); but in some there are no roots, the pulp-cavity being open below

(*I*), and the tooth constantly growing from the base as it becomes worn away at the crown ; such teeth are said to have *persistent pulps.*

Usually Mammals have two distinct sets of teeth developed, the milk and permanent dentitions, but sometimes there is only one, and accordingly we distinguish *diphyodont* and *monophyodont* Mammals: in nearly all of the latter, however, a second set are developed, though they early become absorbed or remain in the condition of functionless vestiges; and in a considerable number of groups it has been stated that more than two sets of teeth

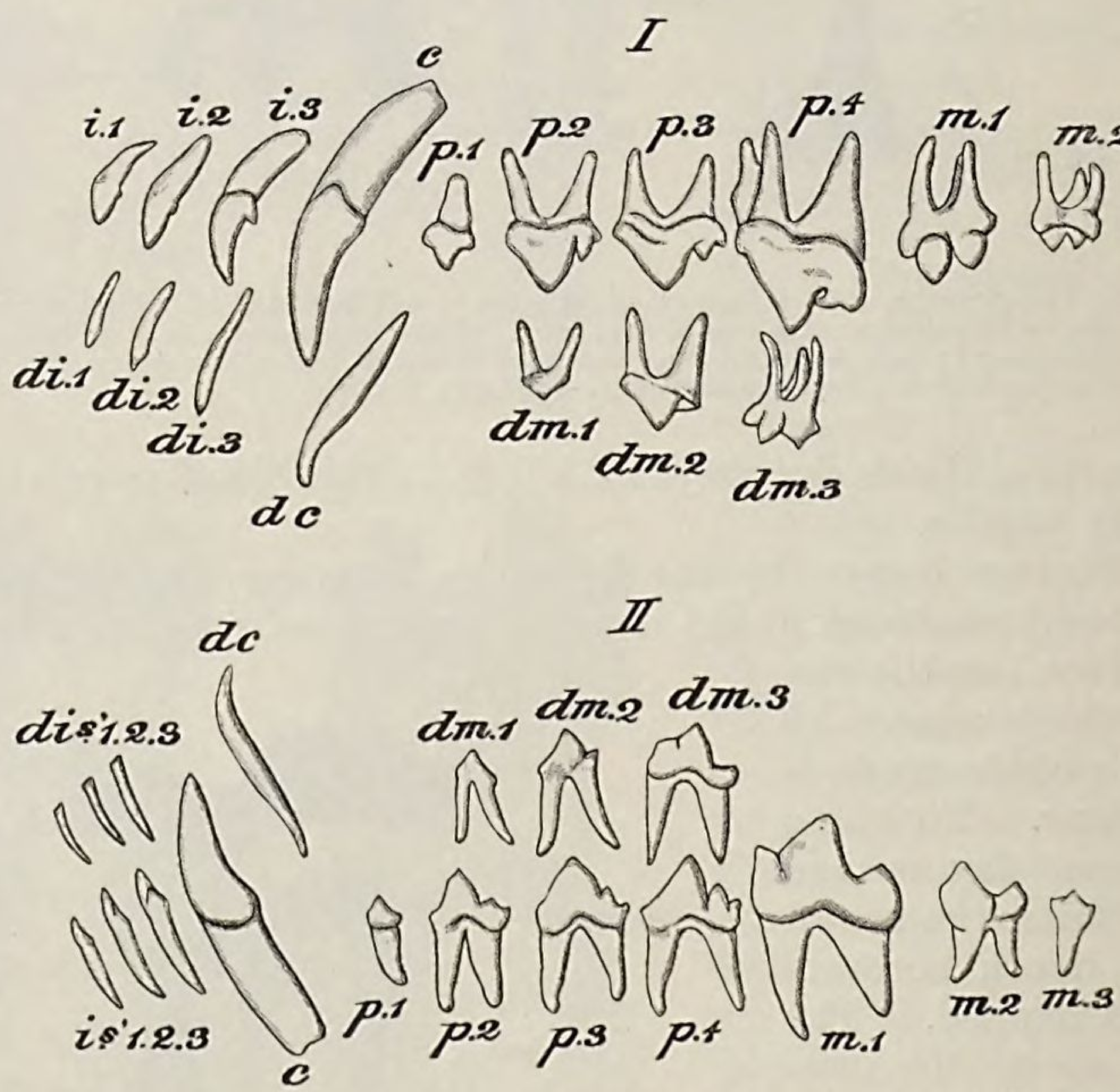


FIG. 1115.—Milk and permanent dentition of upper (*I*) and lower (*II*) of the **Dog** (*Canis familiaris*), with the symbols by which the different teeth are commonly designated. (After Flower and Lydekker.)

are formed, only one, or at most (in diphyodont forms) two, of these sets becoming fully developed. The milk-teeth in Mammals with typical diphyodont dentition sometimes disappear at an early stage, and sometimes do not become replaced by the permanent teeth till long after birth. Some Mammals have the teeth almost indefinite in number, *e.g.*, the Dolphins and Porpoises, in which they are all uniform (*homodont*) and not divided into sets (Fig. 1116). In the typical dentition there are forty-four teeth, viz., three incisors on each side above and below, one canine and seven pre-molars and molars. The incisors (Fig. 1115, *i.*) of the upper jaw are to be distinguished as being the teeth that are lodged in the pre-maxillæ; the incisors of the lower jaw are

the teeth that are placed opposite to these. The upper canine (*s.*) is the most anterior tooth of the maxilla situated on or immediately behind the premaxillo-maxillary suture, and has usually a characteristic shape. The lower canine is the tooth which bites in front of the upper canine. The premolars (*p.*) are distinguished from the molars by having milk predecessors (*d.m.*), but the first premolar is, except in the Marsupials, nearly always a persistent milk-tooth; the molars (*m.*) have no teeth preceding them, and are sometimes looked upon as persistent teeth of the first set. The various sets of teeth are also usually distinguishable by

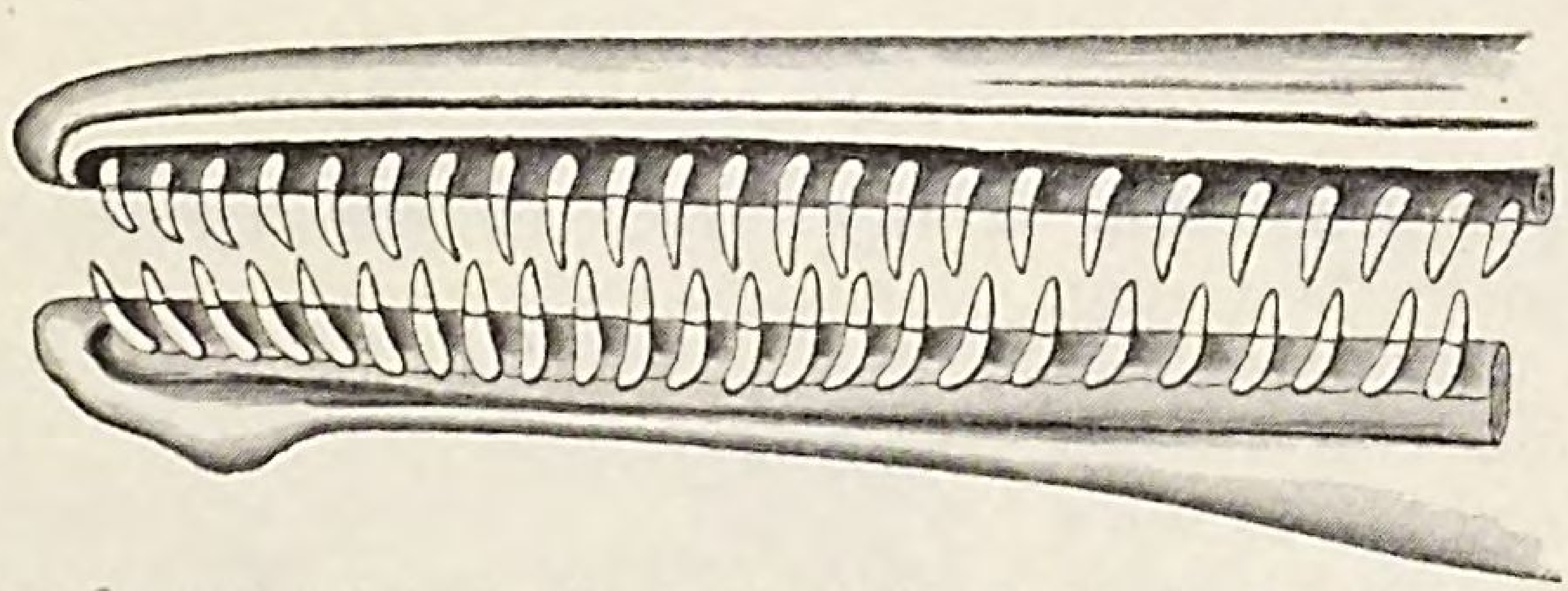


FIG. 1116.—Upper and lower teeth of one side of the mouth of a **Dolphin** (*Lagenorhynchus*), illustrating the homodont type of dentition in a Mammal. (After Flower and Lydekker.)

their shape. As a rule the incisors are teeth with cutting edges; the canines are pointed and conical, the premolars and molars have broad surfaces with ridges and tubercles for crushing the food, and may have from two to four roots.

The simplest form of molar tooth (occurring, however, only in certain extinct forms) is that of a simple cone, or a cone with two small accessory processes or cusps. Almost as primitive is the type of tooth termed *triconodont* (likewise occurring only in a few extinct Mammals), in which there are three equal conical cusps set in a straight line, the upper teeth biting on the outer side of the lower. From the triconodont is derivable the *tritubercculate* molar, in which the free surface of the tooth presents three cusps or tubercles arranged in a triangle, the apex of which is internal in the upper, external in the lower jaw. In the upper molar the inner cusp is termed the *protocone*, the antero-external the *paracone*, and the postero-external the *metacone*. These terms are modified in the case of the molars of the lower jaw, the equivalent of the protocone, here external, being termed the *protoconid* and the others *paraconid* and *metaconid* respectively. This trituberculate type of molar is usually complicated by various additions and modifications—accessory cusps being added, together with ridges or folds connecting the cusps together. The resulting complex tooth may be modified to act as a cutting (*secodont*) or a crushing (*bunodont*) molar. A modification of the bunodont molar is brought about by the cusps, instead of retaining their conical form, being drawn out into the shape of a crescent (*selenodont*).

The number of the various sets of teeth in the jaws is conveniently expressed by a *dental formula*, in which the kind of tooth (incisor, canine, pre-molar, molar) is indicated by the initial letter (*i.*, *c.*, *p.*, *m.*), and the whole formula has the arrangement of four vulgar fractions, in each of which the numerator indicates the teeth of the upper, the denominator those of the lower jaw. Thus:

$$i.\ \frac{3\cdot3}{3\cdot3},\ c.\ \frac{1\cdot1}{1\cdot1},\ p.\ \frac{4\cdot4}{4.4},\ m.\ \frac{3\cdot3}{3\cdot3} = 44,$$

or, in a simpler form, since the teeth of the right and left sides are always the same—

$$i.\ \frac{3}{3},\ c.\ \frac{1}{1},\ p.\ \frac{4}{4},\ m.\ \frac{3}{3} = 44$$

Echidna has no teeth at any stage. In Ornithorhynchus teeth are present in the young, but are early absorbed, and the function of teeth is performed in the adult by broad horny plates, two on the upper and two on the lower jaw.

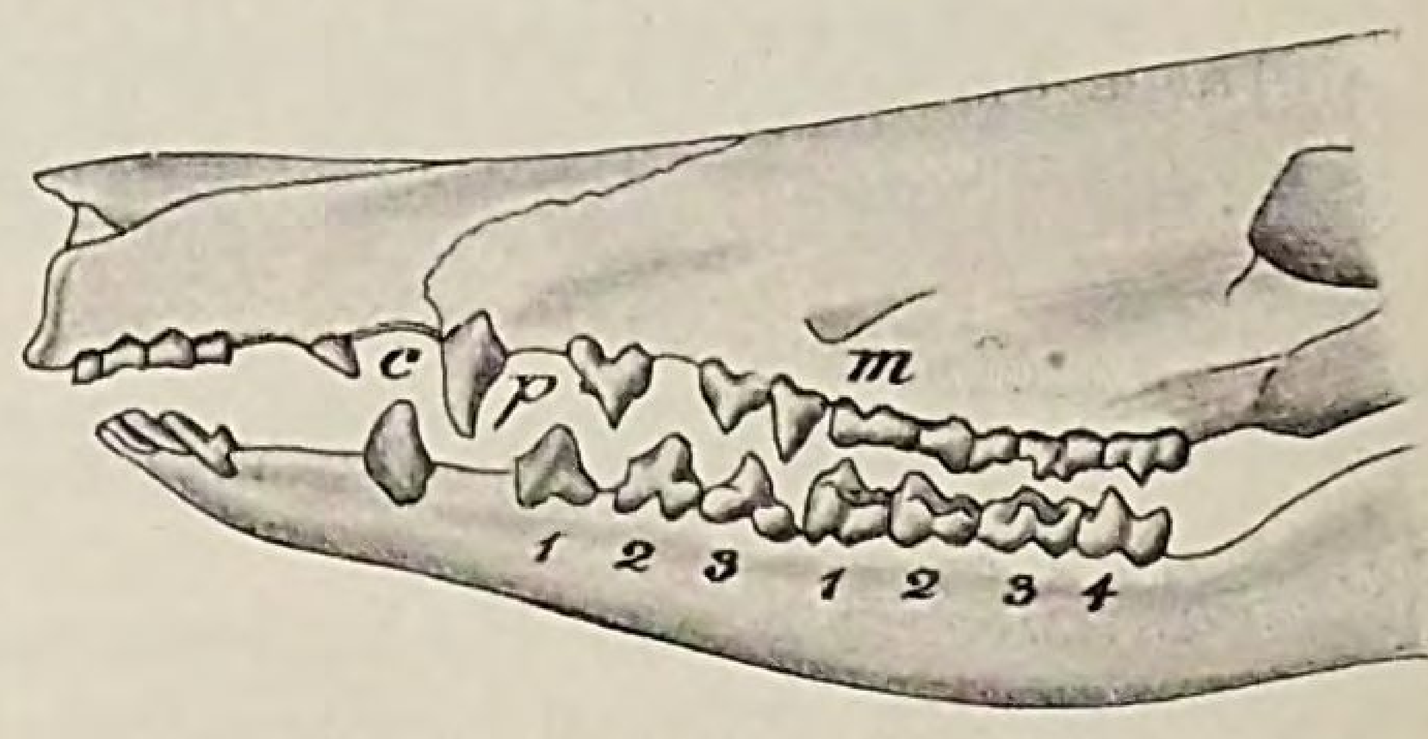


FIG. 1117.—Teeth of **Bandicoot** (*Perameles*). (After Owen.)

The Marsupials have the milk dentition in a degenerate condition. Germs of milk teeth are developed, but with the exception of one, the last pre-molar, and in some cases of canine and incisors, these remain in an imperfect state of development, though they persist, as functionless vestiges, to a comparatively late stage.

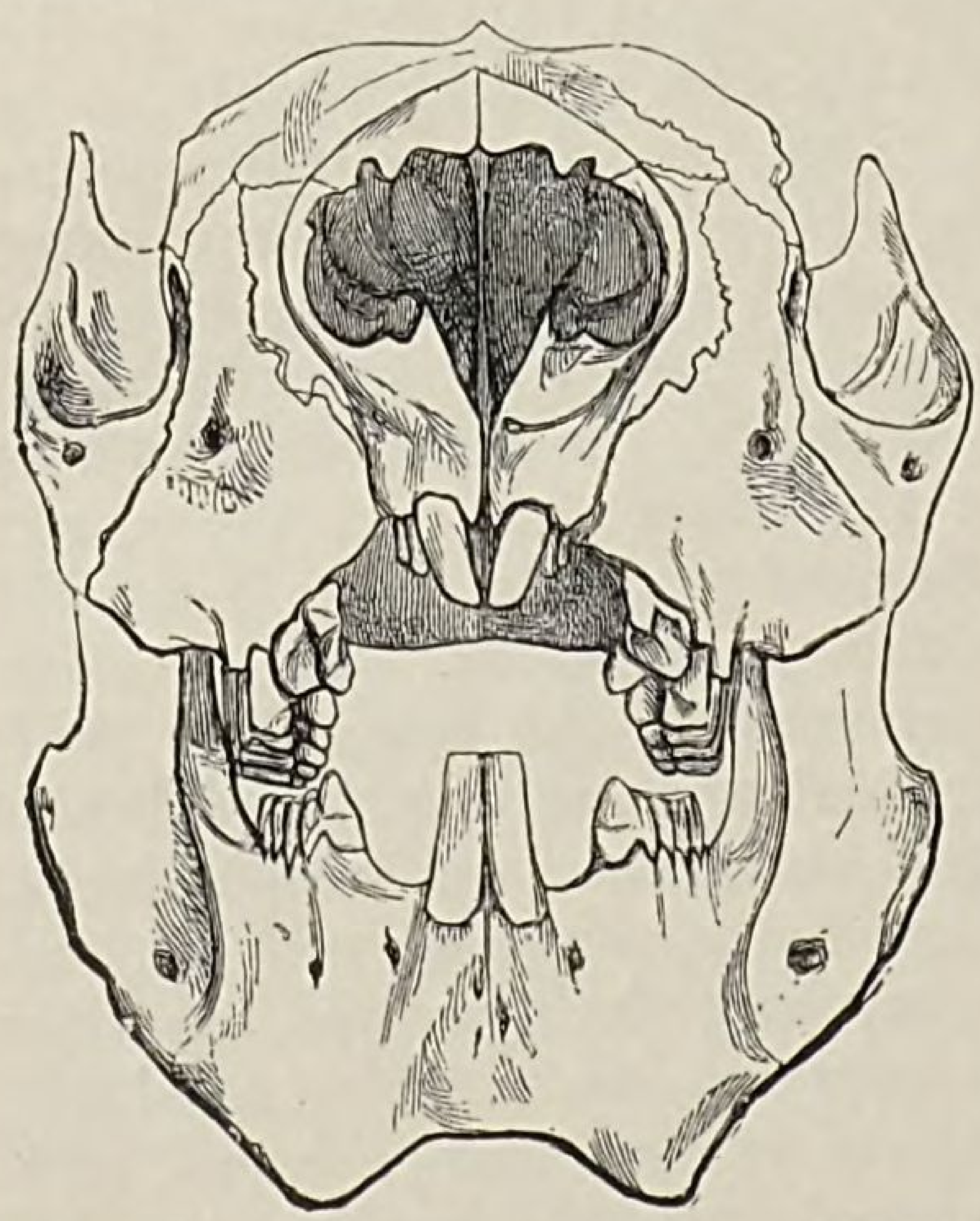


FIG. 1118.—Front view of skull of **Koala** (*Phascolarctos cinereus*), illustrating diprotodont and herbivorous dentition. (After Flower.)

In the adult dentition of the Marsupials the number of incisors in the upper and lower jaws is always dissimilar except in *Phascolomys*. With regard to the arrangement of these teeth, the order falls into two series termed respectively the *diprotodont* and the *polyprotodont*. In the former (Figs. 1118–1119) the two anterior incisors are large and prominent, the rest of the incisors and the canines being smaller or absent. On the other hand, in the polyprotodont forms, which

are all more or less carnivorous, the incisors are numerous and sub-equal and the canines large. There are typically three pre-molars

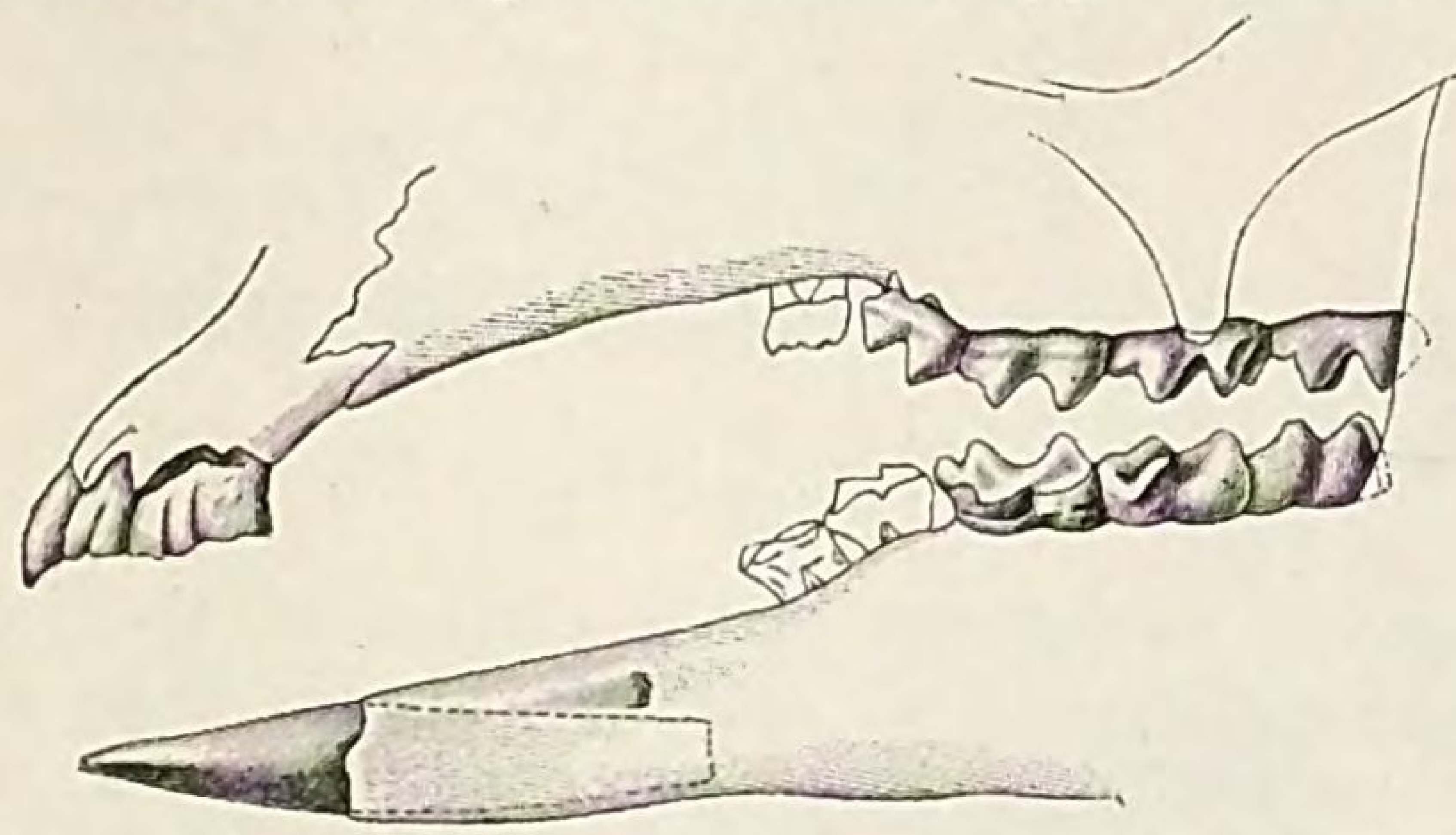


FIG. 1119.—Teeth of **Great Kangaroo** (*Macropus major*)] [(After Owen.)

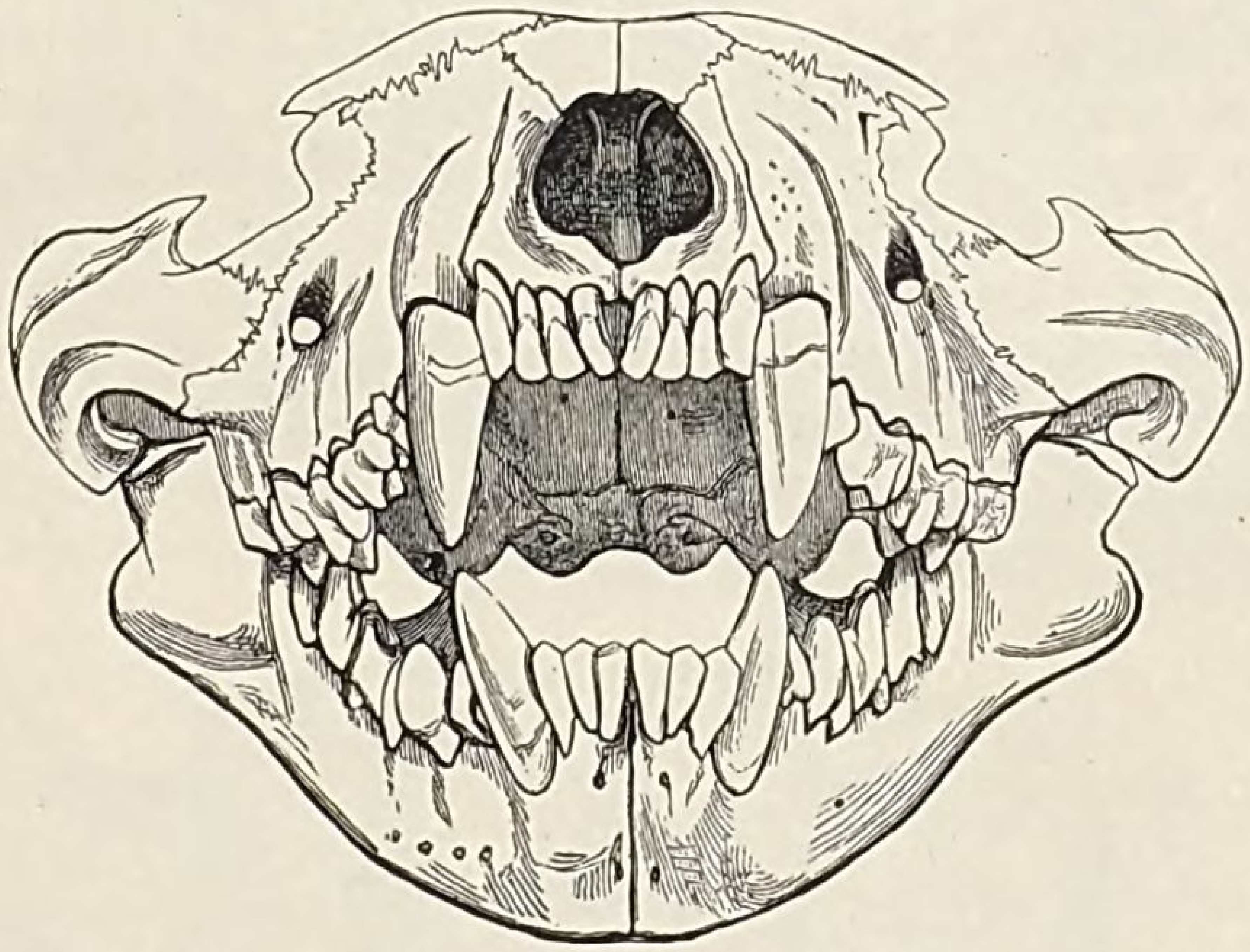


FIG. 1120.—Front view of the skull of **Tasmanian Devil** (*Sarcophilus ursinus*), showing polyprotodont and carnivorous dentition. (After Flower.)

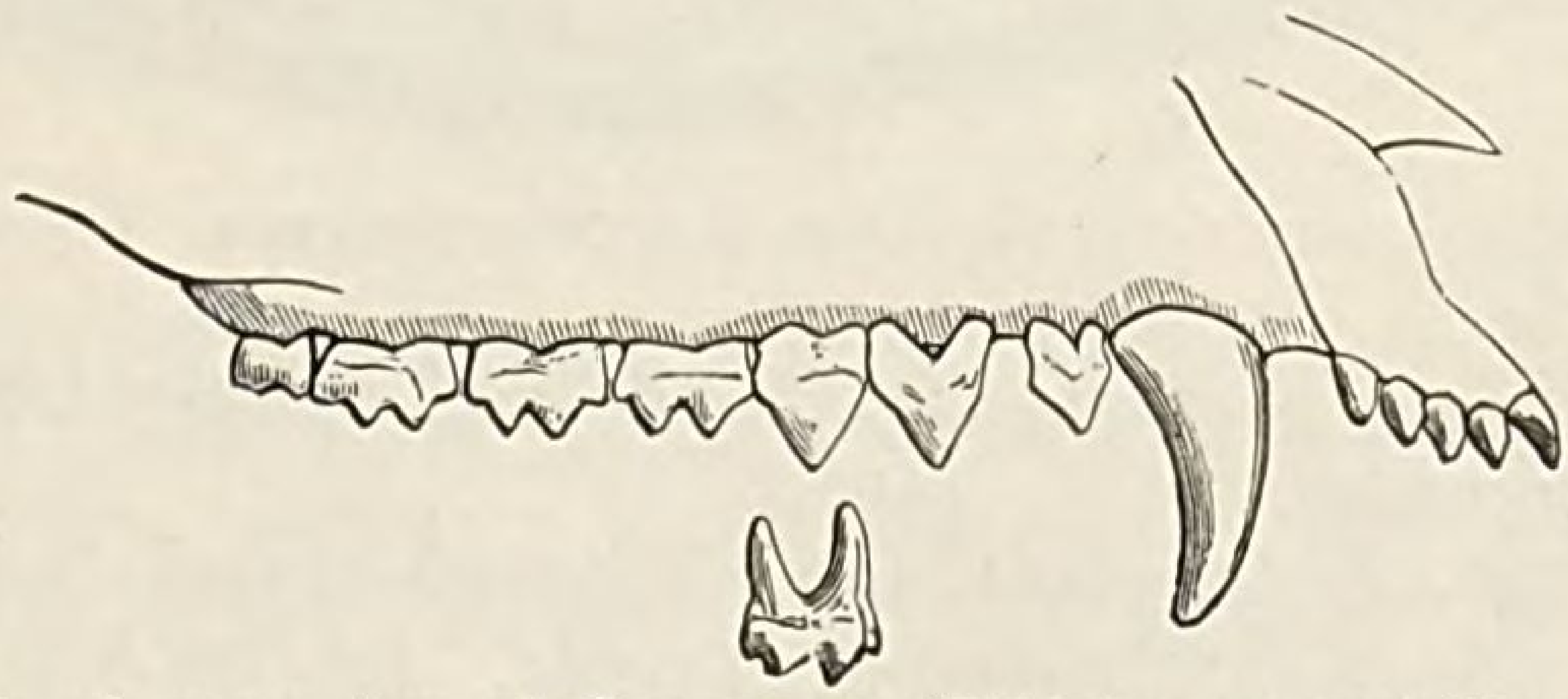


FIG. 1121.—Teeth of upper jaw of **Opossum** (*Didelphys marsupialis*), all of which are unchanged except the last premolar, the place of which is occupied in the young animal by a molariform tooth represented in the figure below the line of the other teeth. (After Flower and Lydekker.)

and four molars. A good example of the diprotodont arrangement is the Kangaroo (Macropus) (Fig. 1119), which has the dental formula—

$$i. \frac{3}{1}, c. \frac{1}{0}, p. \frac{2}{2}, m. \frac{4}{4} = 34.$$

The canine is very small and early lost. Of the polyprotodont forms (Fig. 1120) the Australian Dasyure or Native Cat has the formula—

$$i.\ \frac{4}{3},\ c.\ \frac{1}{1},\ p.\ \frac{2}{2},\ m.\ \frac{4}{4} = 42;$$

and the American Opossum (*Didelphys*) (Fig. 1121)—

$$i.\ \frac{5}{4},\ c.\ \frac{1}{1},\ p.\ \frac{3}{3},\ m.\ \frac{4}{4} = 50.$$

The Edentata, as noticed in the outline of the classification, though not by any means all toothless, always have some defect in the dentition; when teeth are present in the adult the anterior series are absent and the teeth are imperfect, wanting roots and often devoid of enamel. The tooth-characters differ widely in the different groups. In the Sloths there are five teeth above and four below on each side; no second series is known. In the American Anteaters there are no teeth in the adult. In the Armadillos, on the other hand, the teeth are numerous, though simple and rootless, and in one genus at least two series occur. In the Scaly Anteaters there are no teeth. In the Cape Anteaters (Fig. 1122) again there are numerous teeth which are heterodont and diphyodont and have a peculiar structure, being perforated by numerous minute parallel vertical canals; the pulp

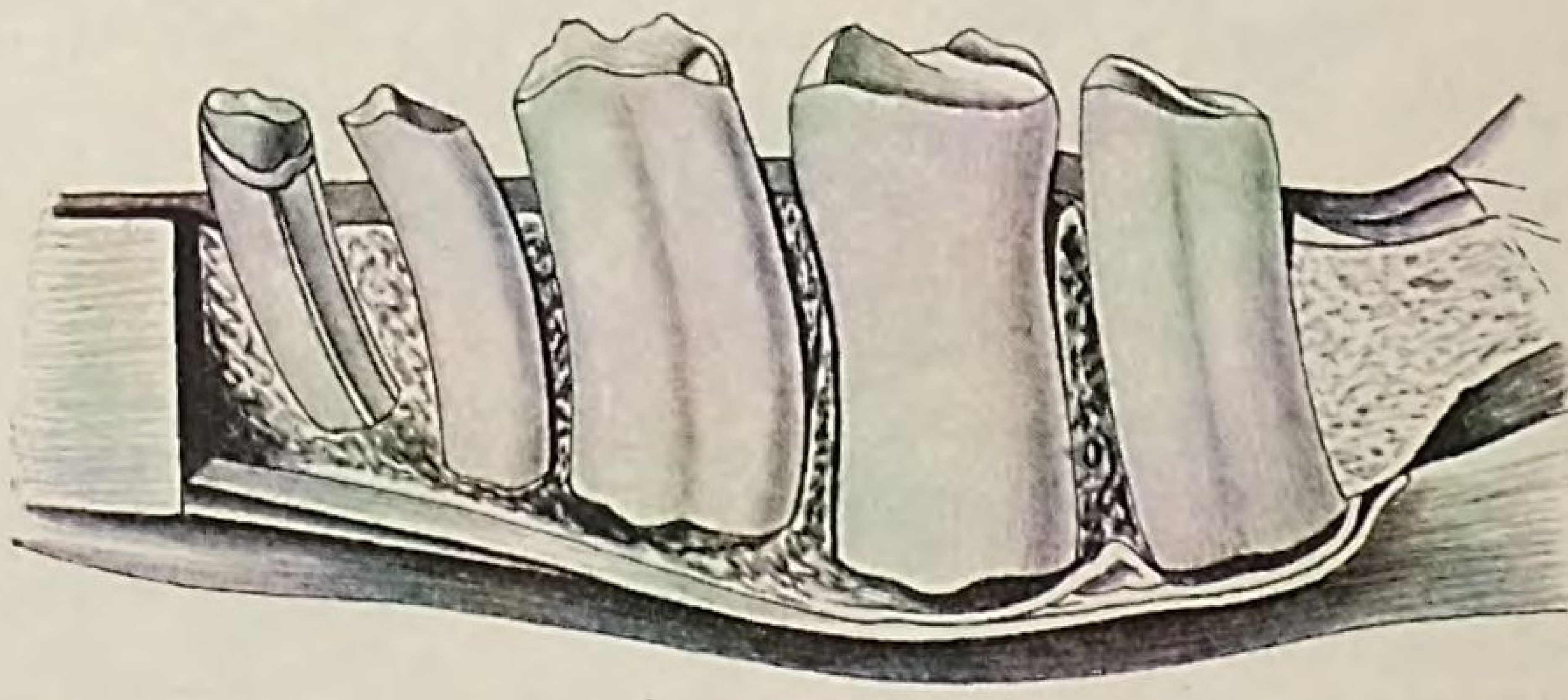


FIG. 1122.—Section of lower jaw and teeth of **Orycteropus**. (After Owen.)

of each tooth, entire at its base, is divided distally into a number of parallel columns.

In the Ungulata the dentition is heterodont and diphyodont, and the teeth are very rarely devoid of roots. In the Artiodactyla the premolars and molars differ from one another in pattern; the first upper pre-molar is almost always without a milk predecessor. The Pigs (Fig. 1123) are among the very few recent Mammalia which possess what has been referred to as a typical dentition: the formula of the completed dentition is—

$$i.\ \frac{3}{3},\ c.\ \frac{1}{1},\ p.\ \frac{4}{4},\ m.\ \frac{3}{3} = 44.$$

The incisors of the upper jaw are vertical, those of the lower greatly inclined forwards. The canines are greatly developed, especially in the male, and grow from persistent pulps; both upper and lower are bent upwards and outwards and work against one another in such a manner that the upper wears on its anterior and external surface, the lower at the extremity of the posterior. The

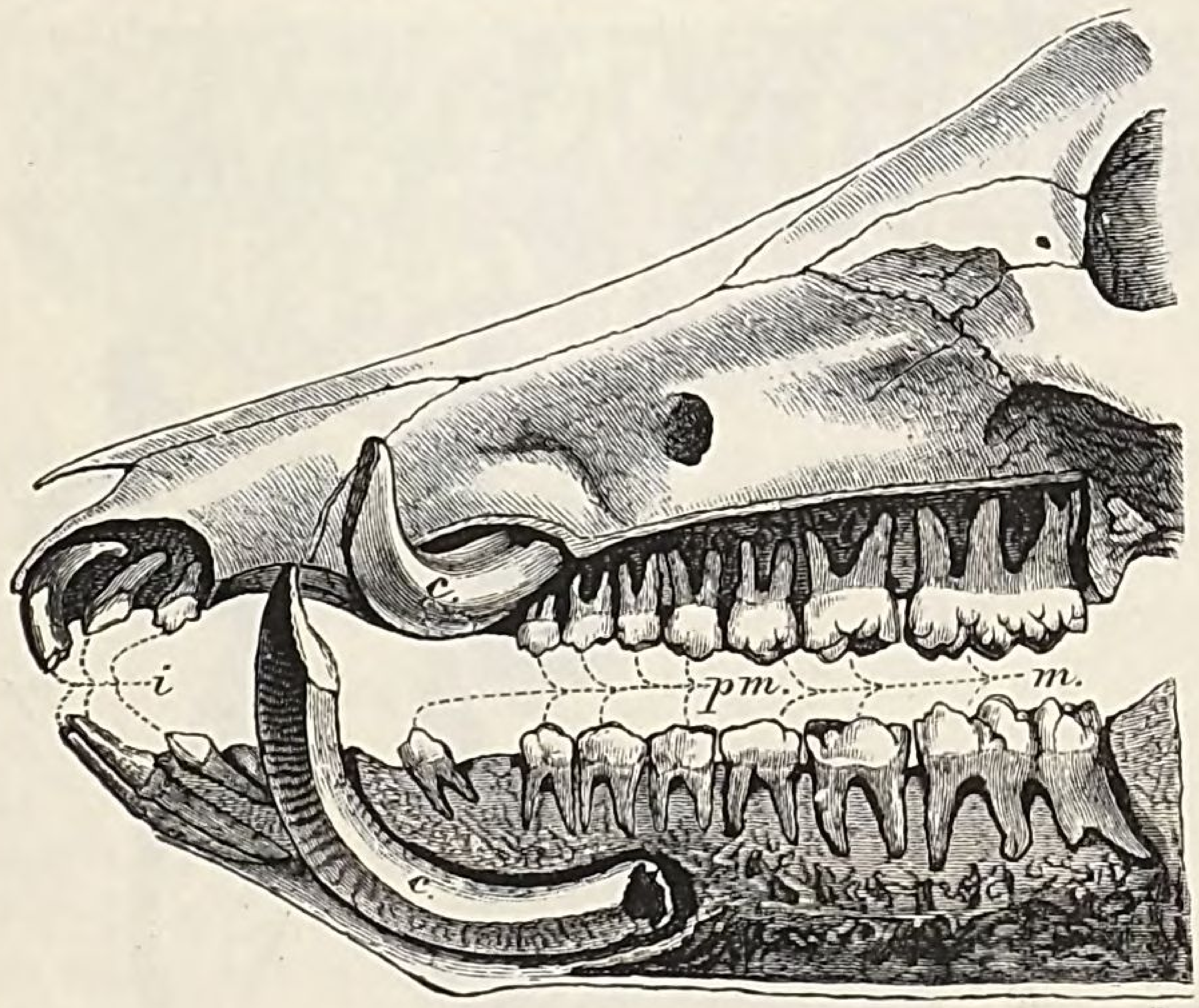


FIG. 1123.—Left lateral view of the dentition of the **Boar** (*Sus scrofa*), the roots of the teeth being exposed. (After Flower and Lydekker.

pre-molars are compressed with longitudinal cutting edges, the molars are provided with numerous tubercles or cusps arranged for the most part in transverse rows. The formula of the milk dentition is—

$$i. \frac{3}{3}, c. \frac{1}{1}, m. \frac{3}{3} = 28.$$

In the typical Ruminants there are no teeth on the pre-maxillæ, the incisors of the lower jaw and the canines, which resemble them in shape, biting against a thickened callous pad on the opposed surface of the upper jaw, and the upper canines are also usually absent; there are three pre-molars and three molars in both upper and lower series, all characterised by the presence of column-like vertical folds of enamel, the interstices between which may be filled up with cement (Fig. 1112, *V*). In the Camels there are a pair of upper incisors and a pair of large canines in each jaw.

In the Perissodactyla the molars and pre-molars form a continuous series of large teeth with ridged or complexly-folded crowns, the posterior pre-molars often differing little in size

and structure from the molars. In the Horse (Fig. 1124) the formula is—

$$i.\ \frac{3}{3},\ c.\ \frac{1}{1},\ p.\ \frac{4}{4},\ m.\ \frac{3}{3} = 44,$$

but the first premolar is a small tooth which soon becomes lost, and may belong to the milk dentition. A fold of the enamel dips downwards (*i.e.* towards the root) from the extremity of the incisor teeth like the partly inverted finger of a glove; the canines are small in the female, and may not appear on the surface. There is a wide interval in both jaws between the canines

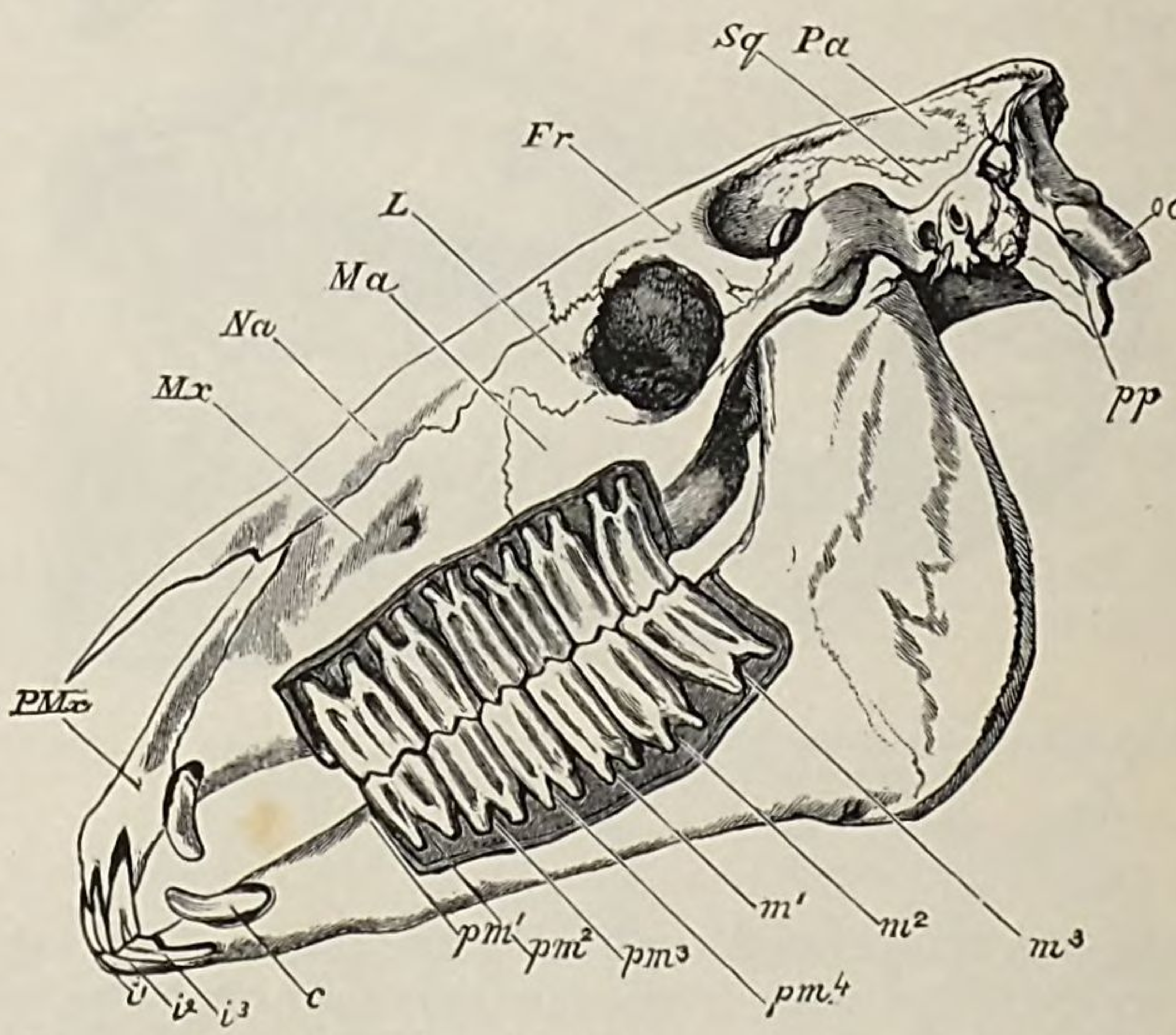


FIG. 1124.—Side view of skull of **Horse** with the bone removed so as to expose the whole of the teeth. *c.* canine; i_1. i_2. i_3. incisors; m^1. m^2. m^3. molars; *p.* m^1. situation of the vestigial first pre-molar, which has been lost in the lower, but is present in the upper jaw; pm^2.pm^3.pm^4. remaining pre-molars; *fr.* frontal; *ju.* jugal; *lcr.* lacrymal; *max.* maxilla; *na.* nasal; *pa.* parietal; *par.oc.* par-occipital process; *p.max.* pre-maxilla; *oc. cond.* occipital condyle; *sq.* squamosal. (After Flower and Lydekker.)

and pre-molars. The pre-molar and molar teeth present a complicated pattern due to folds of the enamel, which differ in their arrangement in the upper and lower jaws; their roots become completed only at a late period.

In the Hyracoidea the dental formula is—

$$i.\ \frac{1}{2},\ c.\ \frac{0}{0},\ p.\ \frac{4}{4},\ m.\ \frac{3}{3} = 34.$$

The upper incisors are not unlike the larger pair of the Rabbit in shape, though prismatic and pointed, instead of compressed and chisel-like, and grow from persistent pulps. The outer incisors are elongated, inclined forwards, and trilobed at the extremities.

The pre-molars and molars form a continuous series, separated by an interval from the incisors, and in pattern closely resemble those of some of the Perissodactyla.

The Elephants (Fig. 1125) have an extremely specialized dentition. There are no canines and no lower incisors. The single

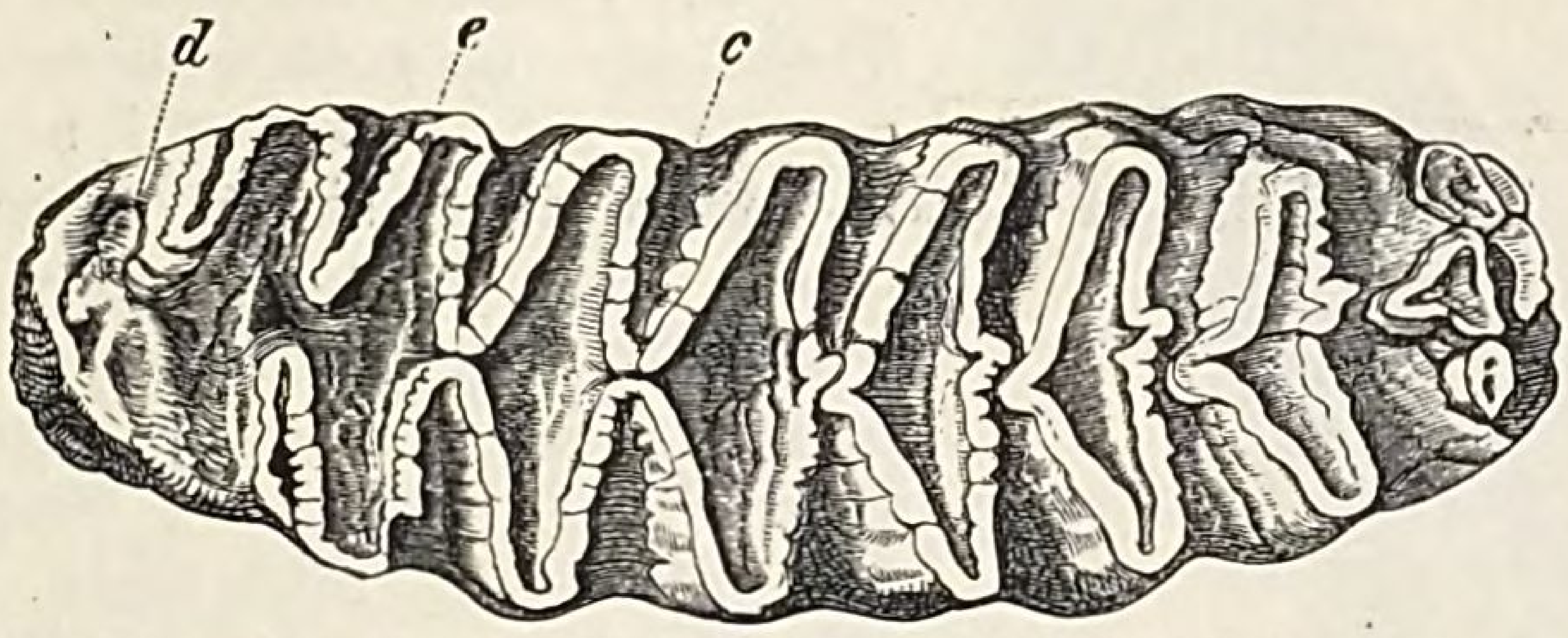


FIG. 1125.—Grinding-surface of a partially worn right upper molar of the **African Elephant** (*Elephas africanus*). (After Owen.)

pair of upper incisors are developed into the enormous tusks (Fig. 1112, *I*), which grow continuously from persistent pulps throughout the life of the animal; they are of elongated conical form, and usually become curved. The tusks are composed of solid dentine, enamel occurring only on the apices, and becoming early worn away. The molars (Fig. 1125) are very large, and their worn surfaces are marked with prominent transverse ridges; there are six molars altogether on each side, but only one or two are functional at once, the more posterior moving forward and taking the place of the more anterior as these become worn out.

When teeth are developed in the Cetacea they are nearly always numerous, homodont, and monophyodont; in the Sperm-whales they are confined to the lower jaw. In the Whale-bone

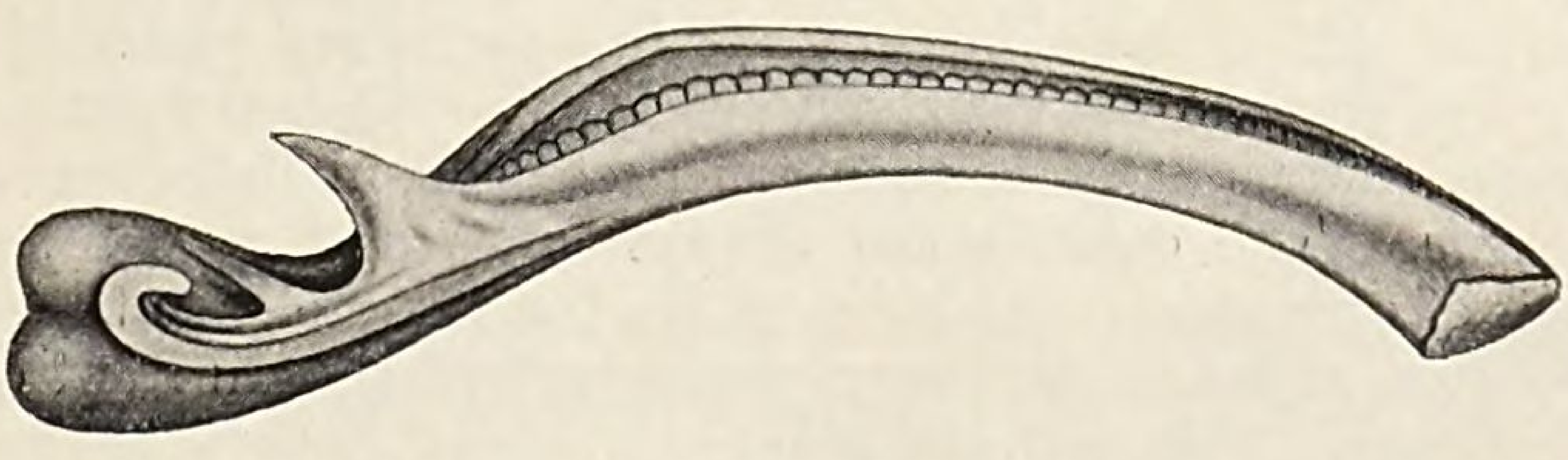


FIG. 1126.—Left lower jaw of fœtus of **Balænoptera rostrata,** inner aspect, size; showing teeth, natural aspect. (After Julin.)

Whales, though teeth are developed in the fœtal condition (Fig. 1126), they become lost either before or soon after birth, and their place is taken in the adult by the plates of baleen or whalebone (Fig. 1127), which, in the form of numerous triangular plates, hang vertically downwards from the palate.

Of the Sirenia, the Dugong and Manatee have a heterodont

dentition; in Rhytina teeth were absent. In the two former Sirenians there are incisors and molars with a wide diastema between them. In the Manatee there are two rudimentary incisors on each side, both in the upper and the lower jaw; these disappear before the adult condition is reached. There are altogether eleven molars on each side above and below, but not more than six of these are in use at once, the more anterior when worn out being succeeded by the more posterior. They have enamelled crowns with transverse ridges, and are preceded by milk teeth. In the Dugong there are no incisors in the mandible of the adult, but one tusk-like pair in the upper jaw, large in the male, in which they grow from persistent pulps, little developed in the female, and remaining concealed in their sockets. In the young there are rudimentary incisors in the mandible, and also a rudimentary second pair in the upper jaw. There are either five or six molars on each side, both in the upper and lower jaws. These are cylindrical teeth, devoid of enamel, and with persistent pulps.

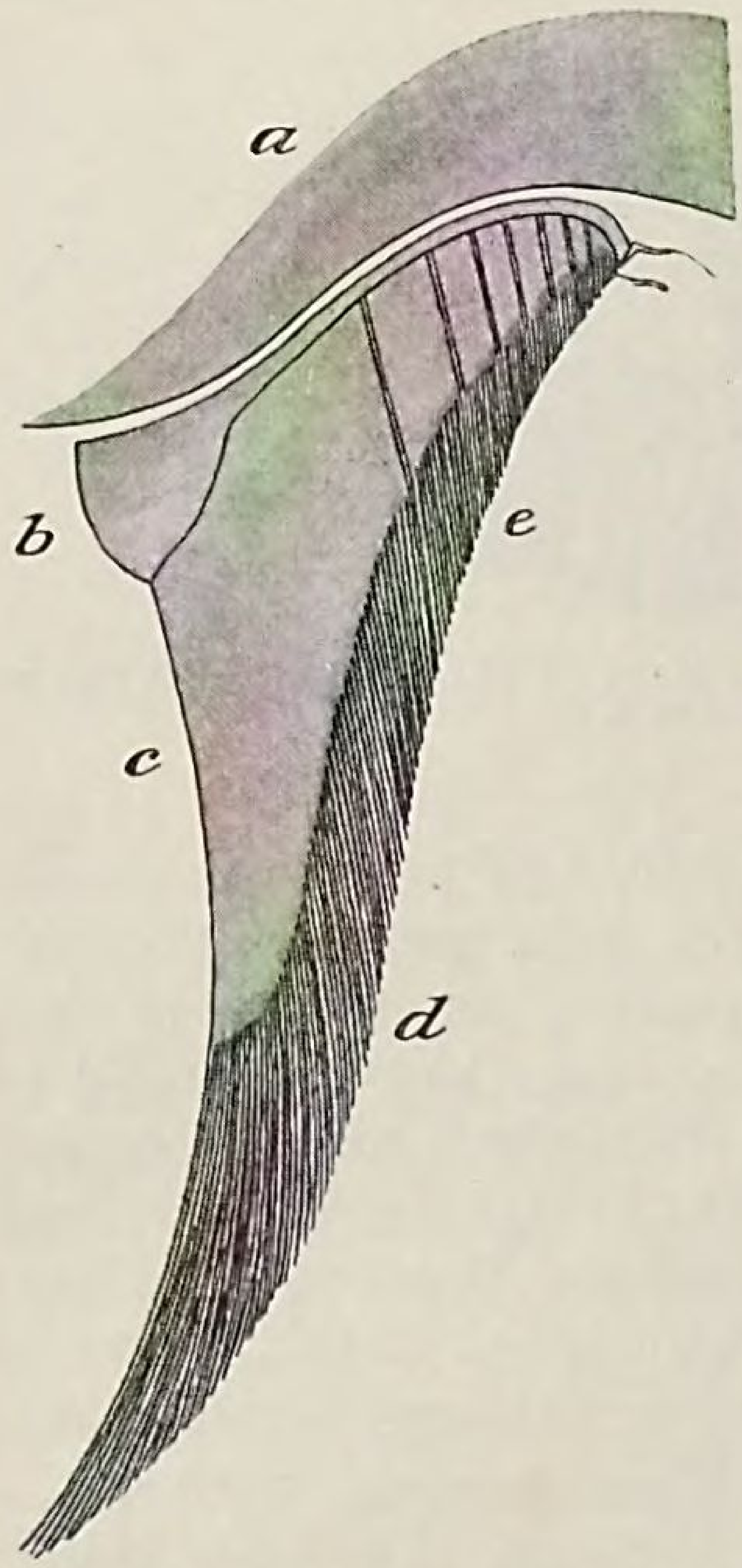


FIG. 1127.—Section of upper jaw, with baleen-plates, of **Balænoptera.** (After Owen.)

In the Carnivora vera (Fig. 1128) the dentition is complete, heterodont and diphyodont, and all the teeth are provided with roots. The incisors are relatively small, chisel-shaped teeth; there are nearly always three of them on each side, in both upper and lower jaws. The canines are always large and pointed. The presence of carnassials, consisting of the last pre-molar in the upper, and the first molar in the lower, jaw, is universal. In front of this the teeth are compressed and pointed; behind it they have broad tuberculated surfaces. In the Cat family (*Felidæ*) the formula is—

$$i.\ \frac{3}{3},\ c.\ \frac{1}{1},\ p.\ \frac{3}{2},\ m.\ \frac{1}{1} = 30.$$

The lower carnassial is thus the last of the series. In the Dogs (Canidæ) the formula is usually—

$$i.\ \frac{3}{3},\ c.\ \frac{1}{1},\ p.\ \frac{4}{4},\ m.\ \frac{2}{3} = 42,$$

and in the Bears (Ursidæ) it is the same.

In the Pinnipedia there are always fewer than $\frac{3}{3}$ incisors, and carnassials are not developed. The pre-molars and molars have a compressed conical pointed form. The prevailing dental formula of the Seals is—

$$i. \frac{3}{2}, c. \frac{1}{1}, p. \frac{4}{4}, m. \frac{1}{1} = 34.$$

In the Walrus the adult formula is—

$$i. \frac{1}{0}, c. \frac{1}{1}, p. \frac{3}{3}, m. \frac{0}{0} = 18.$$

The upper canines take the form of large, nearly straight tusks.

In the large order of the Rodents the dentition is remarkably uniform, and, in all its general characters, resembles what has

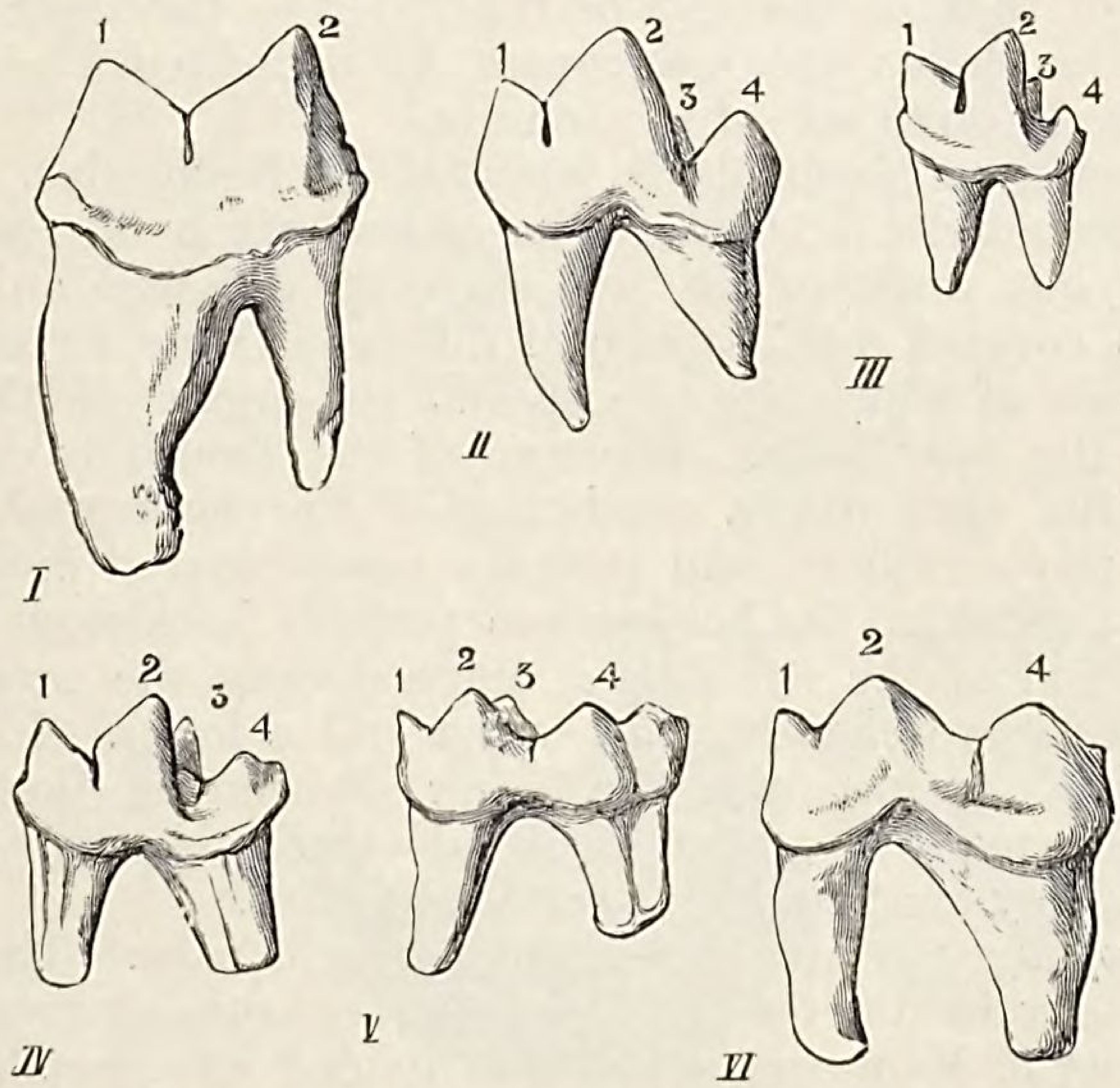


FIG. 1128.—Left lower carnassial teeth of **Carnivora.** *I*, **Felis**; *II*, **Canis**; *III*, **Herpestes**; *IV*, **Lutra**; *V*, **Meles**; *VI*, **Ursus.** 1, anterior lobe (paraconid) of blade; 2, posterior (protoconid) lobe of blade; 3, inner cusp (metaconid); 4, talon (hypoconid.) (After Flower and Lydekker.)

already been described in the Rabbit. But the second, smaller pair of incisors of the upper jaw is present only in the Hares and Rabbits; the number of pre-molars and molars varies from—

$$p. \frac{0}{0}, m. \frac{2}{2} \text{ to } p. \frac{3}{2}, m. \frac{3}{3},$$

and they may develop roots.

In the Insectivora the dentition is heterodont, complete, and

diphyodont. All the teeth are rooted. There are never fewer than two incisors on either side of the lower jaw. The canines are not of large size. The crowns of the molars are beset with pointed tentacles.

In the Chiroptera the dentition is complete, and the teeth are all rooted. There is a milk series which differs entirely from the permanent teeth. In the insectivorous Chiroptera (Bats) the molars are provided with pointed cusps, while in the frugivorous forms (Flying Foxes) they are longitudinally grooved or excavated.

In the Primates the teeth are heterodont and diphyodont, and always form roots. There are almost invariably two incisors on each side in each jaw, and in all but the Hapalidæ three molars. The dental formulæ of the various families have been given in the synopsis of the classification. The dentition of Man differs from that of the rest of the order in the teeth forming a continuous series not interrupted by a diastema, and in the comparatively small size of the canines.

The mouth in Mammals is bounded by fleshy lips. On the floor of the mouth is situated the *tongue*, which is usually well developed, but varies in size and shape in different orders. Its surface is covered with papillæ of different forms, in association with certain of which are the special end-organs of the nerves of taste—the *taste bulbs*. The roof of the mouth is formed in front by the *hard palate*, consisting of the horizontal palatine plates of the maxillary and palatine bones covered with mucous membrane. Behind the hard palate projects backwards the soft muscular fold of the *soft palate*, which divides the cavity of the pharynx into two chambers, an upper and a lower. In front of the opening, leading from the lower division of the pharynx into the larynx, is a cartilaginous lid—the epiglottis—of which rudiments only are found in lower Vertebrates.

The *œsophagus* is always a simple straight tube. The *stomach* varies greatly in different orders, being sometimes simple, as in the majority of Mammals, sometimes divided into chambers, as in the Cetacea and the Ruminants.

In the majority of Mammals the stomach is a simple sac, as in the Rabbit (p. 431). But in certain groups it is complicated by the development of internal folds, and may be divided by constrictions into a number of different chambers. The complication of this organ reaches its extreme limit in the ruminant Ungulata, and in the Cetacea In a typical Ruminant (Fig. 1129, E, Fig. 1130), such as a Sheep or an Ox, the stomach is divided into four chambers—the *rumen* or *paunch*, the *reticulum*, the *psalterium*, and the *abomasum* or *rennet stomach*. The first of these (*b*) is much larger than the rest; its mucous membrane is beset with numerous short villi. The reticulum (*c*), which

is much smaller than the rumen, has its mucous membrane raised up into a number of anastomosing ridges, giving its wall the appearance of a honeycomb with shallow cells. From the

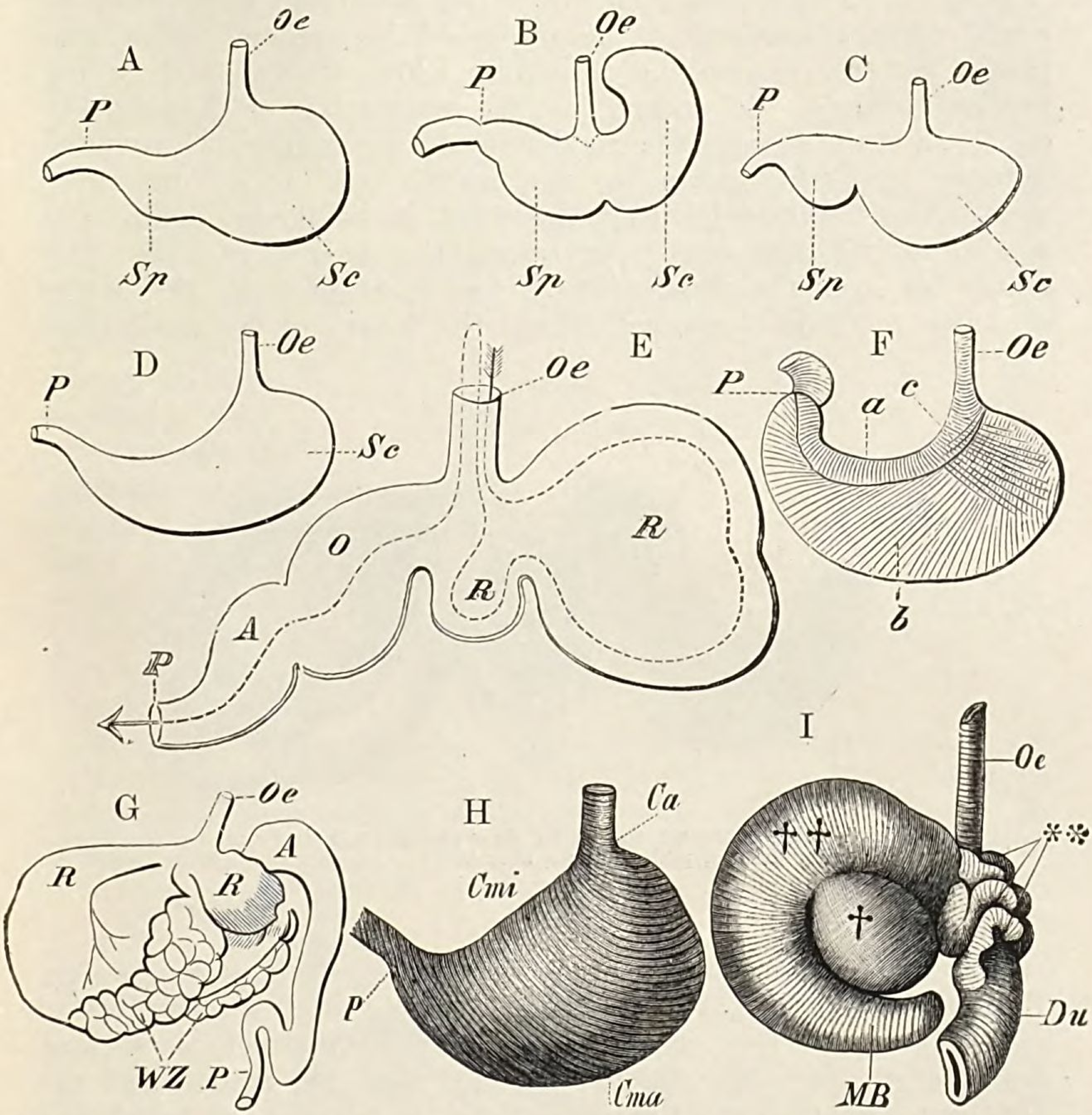


FIG. 1129.—Different forms of the **stomach** in Mammals. *A*, **Dog**; *B*, **Mus decumanus**; *C*, **Mus musculus**; *D*, **Weasel**; *E*, scheme of the **ruminant** stomach, the arrow with the dotted line showing the course taken by the food; *F*, **human** stomach; *G*, **Camel**; *H*, **Echidna aculeata**; *I*, **Bradypus tridactylus.** *A*. (in *E*) abomasum; *Ca*. cardiac end; *Cma*, greater curvature; *Cmi*, lesser curvature; *Du*. duodenum; *MB*, cœcum; *O*, psalterum; *Oe*. œsophagus; *P*. pylorus; *R*. (to the right in Fig. *E*) rumen; *R*. (to the left in Fig. *E*) reticulum; *Sc*. cardiac division; *Sp*, pyloric division; *W. Z*, water-cells. (From Wiedersheim's *Comparative Anatomy*.)

aperture by which the reticulum communicates with the rumen, to that with which it communicates with the psalterium, runs a groove bounded by a pair of muscular ridges, which are capable of closing together in such a way as to convert the groove into a canal. The mucous membrane of the psalterium (*d*) is raised

up into numerous longitudinal leaf-like folds. The abomasum (*e*), smaller than the rumen, but larger than the reticulum, has a smooth vascular and glandular mucous membrane. The œsophagus opens into the rumen close to its junction with the reticulum. The herbage on which the Ruminant feeds is swallowed without mastication, accompanied by copious saliva, and passes into the rumen and reticulum, where it lies until, having finished feeding, the animal begins ruminating or chewing the cud. In this process the sodden food is returned in rounded boluses from the rumen to the mouth, and there undergoes mastication. When fully masticated it is swallowed again in a semi-fluid condition, and passes along the groove into the reticulum, or over the unmasticated food contained in the latter chamber, to strain through between the leaves of the psalterium

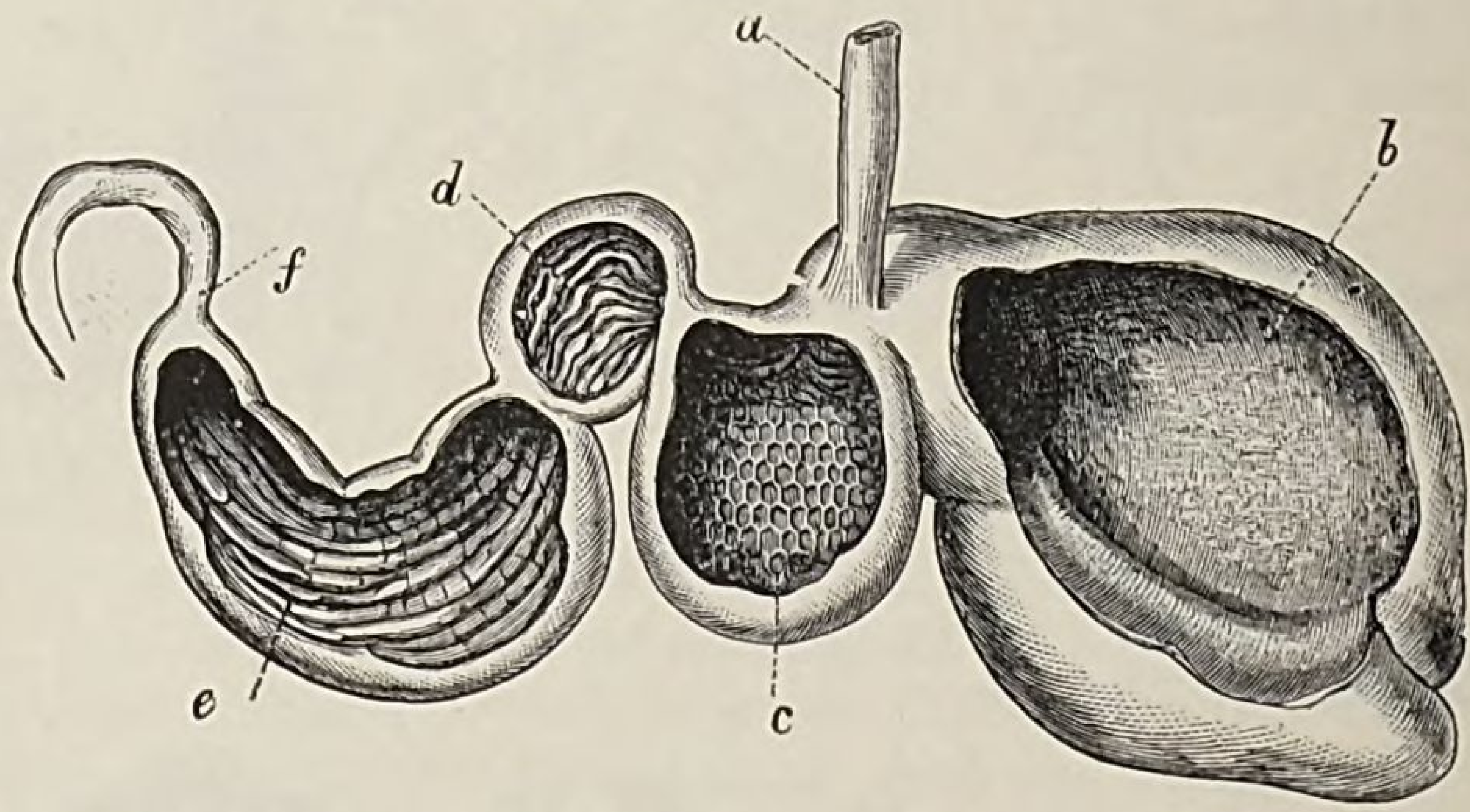


FIG. 1130.—Stomach of **Ruminant** opened to show the internal structure. *a*, œsophagus *b*, rumen; *c*, reticulum; *d*, psalterium; *e*, abomasum; *f*, duodenum. (After Flower and Lydekker.)

and enter the abomasum, where the process of digestion goes on. In the Camels (Fig. 1129, G) the stomach is not so complicated as in the other Ruminants, there being no distinct psalterium, and the rumen being devoid of villi. Both the rumen and the reticulum have connected with them a number of pouch-like diverticula (*w. z.*), the openings of which are capable of being closed by sphincter muscles; in these water is stored. In the Cetacea the stomach is also divided into compartments. In the Porpoise (Fig. 1131) the œsophagus (*a*) opens into a spacious crop (*b*), the cardiac compartment of the stomach, with a smooth, thick, mucous membrane. This is followed by a second chamber (*c*) of considerably smaller dimensions with a glandular mucous membrane, which is thrown into a number of complex folds. A long and narrow third, or pyloric, compartment (*d,e*) follows upon this, terminating in a constricted pyloric aperture, beyond which the beginning of the intestine is dilated into a bulb.

A cœcum situated at the junction of the large and small intestines is usually present, but varies greatly in extent in the different orders and families. It is much larger in vegetable feeding than in carnivorous forms, and among the former it is those that have a simple stomach, such as the Rabbit, that have the largest cæcum. Hyrax differs from all the rest of the class in having a pair of supplementary cœca situated some distance down the large intestine. A cœcum is absent in the Sloths, some Cetacea, and a few Carnivora.

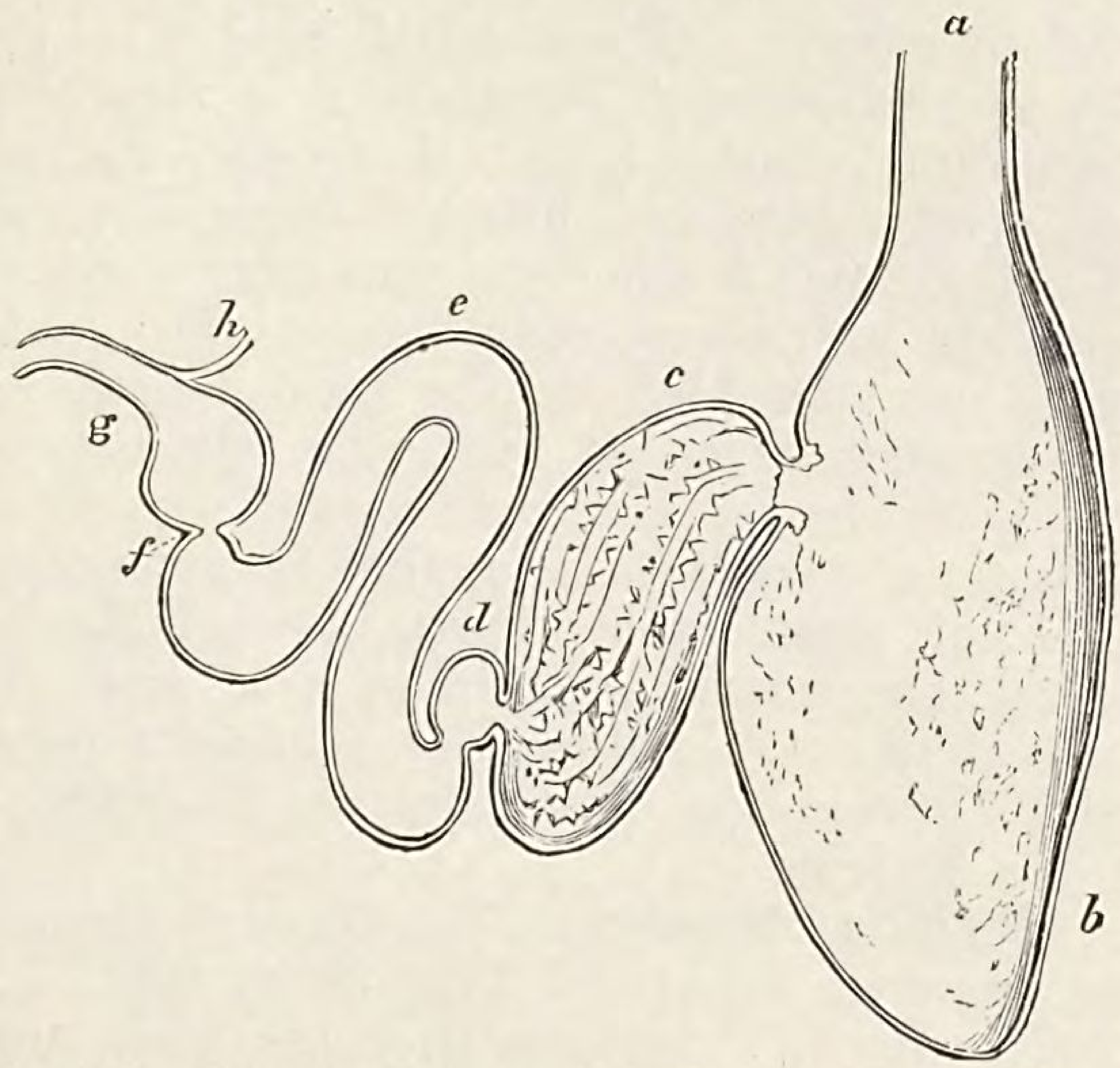


FIG. 1131.—Diagrammatic section of the stomach of the **Porpoise.** *a*, œsophagus; *b*, left or cardiac compartment; *c*, middle compartment; *d* and *e*, the two divisions of the right, or pyloric compartment; *f*, pylorus; *g*, duodenum, dilated at its commencement; *h*. bile-duct. (After Flower and Lydekker).

The Prototheria resemble Reptiles, Birds, and Amphibia, and differ from other Mammals in the presence of a cloaca, into which not only the rectum, but the urinary and genital ducts open. In the Marsupials a common sphincter muscle surrounds both anal and urino-genital apertures; in nearly all the Eutheria the apertures are distinct, and separated from one another by a considerable space—the *perinœum*.

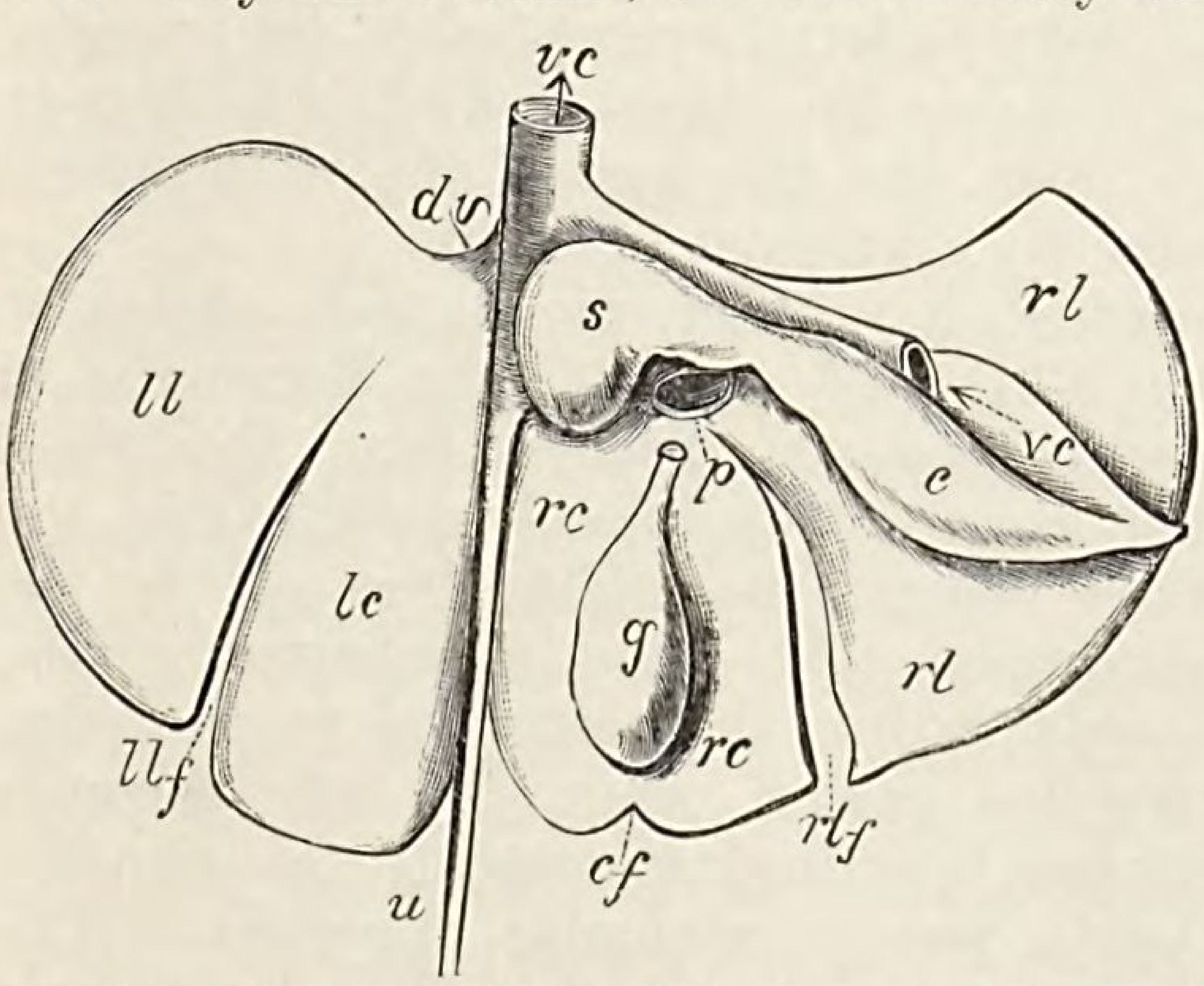


FIG. 1132.—Diagrammatic plan of the liver of a **Mammal** (posterior surface). *c*. caudate lobe; *cf*. cystic fissure; *dv*. ductus venosus; *g*. gall-bladder; *lc*. left central lobe; *ll*. left lateral lobe; *llf*. left lateral fissure; *p*. portal vein entering transverse fissure; *rc*. right central lobe; *rl*. right lateral lobe; *rlf*. right lateral fissure; *s*. Spigelian lobe; *u*. umbilical vein; *vc*, post-caval. (After Flower and Lydekker.)

The liver (Fig. 1132) consists of two parts or *main divisions*, right and left, incompletely separated from one another by a fissure termed *umbilical* owing to its marking the position of the fœtal

umbilical vein. Usually each of these main divisions is divided by a fissure into two parts, so that *right lateral* (*rl.*) and *right central* (*rc.*), and *left lateral* (*ll.*) and *left central* (*lc.*) lobes are distinguishable. When a gall-bladder is present, as is the case in the majority of Mammals, it is attached to, or embedded in, the right central lobe. A fissure, the *portal*, through which the portal vein and hepatic artery pass into the substance of the liver, and the hepatic vein passes out, crosses the right central lobe near the anterior border. The post-caval lies in contact with, or embedded in, the right lateral lobe near its anterior border, and, given off from this lobe between the post-caval and the portal fissure, is a small lobe, of varying extent—the *Spigelian*. The term *caudate lobe* is applied to a process of the right lateral lobe, of considerable extent in most Mammals, having the post-caval vein in intimate relation to it, and often closely applied to the kidney. A gall-bladder is usually present, but is absent in the Cetacea, the Perissodactyle Ungulata, the Hyracoidea, and some Rodents.

Vascular System.—The blood of Mammals is warm, having a temperature always of from 35° to 40° C. The *red corpuscles* are non-nucleated: in form they are most usually biconcave discs, always circular in outline, except in the Camelidæ, in which most of them are elliptical. The *lymphatic system* of vessels is very highly developed, ramifying richly throughout all parts of the body. In the course of this system occur numerous lymphatic glands. The special part of the lymphatic system of vessels (*lacteals*), which ramify in the wall of the intestine and absorb the fatty matters of the food, combine with the lymphatic vessels from the hind limbs and body to form a receptacle—the *receptaculum chyli*—from which a tube, the *thoracic duct*, which may be double, runs forwards to open into the base of one of the great veins of the pre-caval system by a valvular aperture.

The general statements which have been given with regard to the *heart* of the Rabbit (p. 433) hold good for the Mammalia in general. The sinus venosus is never distinct from the right auricle; of its valves, which are more completely retained in the Edentata than in the other orders, the right gives rise to the Eustachian valve, a membranous fold, often fenestrated in the adult, extending from the right wall of the post-caval to the edge of the foramen ovale (annulus ovalis), while the left becomes merged in the auricular septum, helping to complete the annulus ovalis behind. Each auricle has an auricular appendix. The right auriculo-ventricular aperture has a three-lobed tricuspid valve, and the left a two-lobed bicuspid, or mitral, with chordæ tendineæ and musculi papillares. In all, the openings of the pulmonary artery and aorta are provided with three-lobed semi-lunar valves.

The single aortic arch, situated in all Mammals on the left side, varies greatly in the way in which it gives off the main arterial trunks. Sometimes a single large trunk passes forwards from the arch of the aorta and gives rise to both carotids and both subclavians. Sometimes there are two main trunks—*right* and *left innominate arteries*—each giving rise to the carotid and subclavian of its own side. Sometimes there is a right innominate giving off right carotid and right subclavian, the left carotid and left subclavian coming off separately from the arch of the aorta, or, as in the Rabbit, an innominate may give origin to the right subclavian and both carotids, the left subclavian coming off separately.

In Monotremes and Marsupials, in most Ungulates, and in the Rodentia, Insectivora, and Chiroptera, both right and left pre-cavals persist; in the others the left aborts, its vestige giving rise to the coronary sinus. In the Monotremes the openings of all three cavals are provided with valves, only vestiges of which exist in the other groups. In the Monotremes all the pulmonary veins open by a common trunk. In the Metatheria and Eutheria the four veins sometimes open separately, sometimes the two veins of each side unite to form a single lateral trunk.

The following are some of the principal variations in the structure of the heart which occur in the different groups of Mammals. In the Monotremes there is a deep fossa representing the fossa ovalis in the auricular septum. The tricuspid valve in Ornithorhynchus consists of two membranous and two fleshy portions; the mitral valve is wholly membranous. In Echidna the tricuspid valve is completely membranous, and consists of two portions—a larger and a smaller. In the Marsupials the fossa ovalis and annulus ovalis are absent; in the uterine fœtus of the Kangaroo the auricles communicate by a fissure, but all trace of this becomes lost before the adult stage is reached.

In the Cetacea, Eustachian and Thebesian valves are both absent. In some of the Cetacea the apices of the ventricles are separated by a slight depression. In the Sirenia there is a corresponding, but much deeper and wider, cleft, so that the apex of the heart is distinctly bifid.

In the Ungulata, Eustachian and coronary valves are both absent; in some there is a cartilage or a bone—the *os cordis*—often double, at the base of the heart. The Eustachian valve is absent in most of the Carnivora. In the Pinnipedia, an aperture of communication between the auricles often persists in the adult.

The **organs of respiration** resemble those of the Rabbit in the general features mentioned on p. 437.

In the Cetacea, the epiglottis and arytenoids are prolonged to form a tube, which extends into the nasal chambers, and is embraced by the soft palate, so that a continuous passage is formed,

leading from the nasal chambers to the larynx, and giving rise to the condition of *intra-narial epiglottis.* In all the remaining orders a similar condition occasionally occurs. In fœtal Marsupials, in which the intra-narial condition is very complete, it is obviously associated with the passive absorption of the milk, while breathing is being carried on continuously through the nostrils. Some Cetacea and Artiodactyla are exceptional in having a *third bronchus,* which passes to the right lung anteriorly to the ordinary bronchus of that side, and to the pulmonary artery. In connection with various parts of the respiratory system, there are cavities containing air. The connection of the tympanic cavity with the pharynx by means of the Eustachian tubes has been already mentioned. Air-sinuses, connected with the nasal chambers, extend into the bones of the skull, especially into the maxillæ and frontals, where they may reach large dimensions and are known as the *maxillary antra* and *frontal sinuses.* Air sacs are also developed in connection with the larynx in many of the Apes.

Nervous System.—The brain of Mammals (Fig. 1133) is distinguished by its relatively large size, and by the large size and complex structure of the *cerebral hemispheres* of the forebrain.

The cerebral hemispheres of opposite sides are connected together across the middle line in all Mammals, except the Monotremes and Marsupials, by a band of nerve tissue termed the *corpus callosum*—a structure not present in the Sauropsida. The hemispheres, in all but certain of the lower groups of Mammals, are not smooth, but marked by a number of grooves or sulci separating winding ridges or convolutions. The *lateral ventricles* in the interior of the hemispheres are of large size and somewhat complex form.

The *optic lobes,* which are relatively small, are divided into four parts, and are hence called the *corpora quadrigemina.* The *pineal body* is always a small gland-like structure. Connecting together the lateral parts of the cerebellum, which, in the higher Mammals, attains a high degree of development, is a transverse flattened band—the *pons Varolii* (*Po.*)—crossing the hind brain on its ventral aspect.

In the Monotremes and Marsupials (Figs. 1134, 1135) there is no corpus callosum, while the anterior commissure (*ant. com.*) is of relatively large size. The hippocampi extend along the whole length of the lateral ventricles. The layer of nerve-cells in each hippocampus gives origin, as in Eutheria, to numerous fibres, which form a layer on the surface, the *alveus*, and become arranged in a band—the tænia hippocampi. In the Eutheria, as we have seen in the case of the Rabbit, the tæniæ unite mesially to form the body of the fornix. In the Monotremes and Marsupials, on the other

hand, there is no such union; the fibres of the tænia run towards the foramen of Monro, where they become divided into several sets. Of these one set, constituting the great majority of the fibres, pass into the hippocampus of the opposite side, giving rise to a

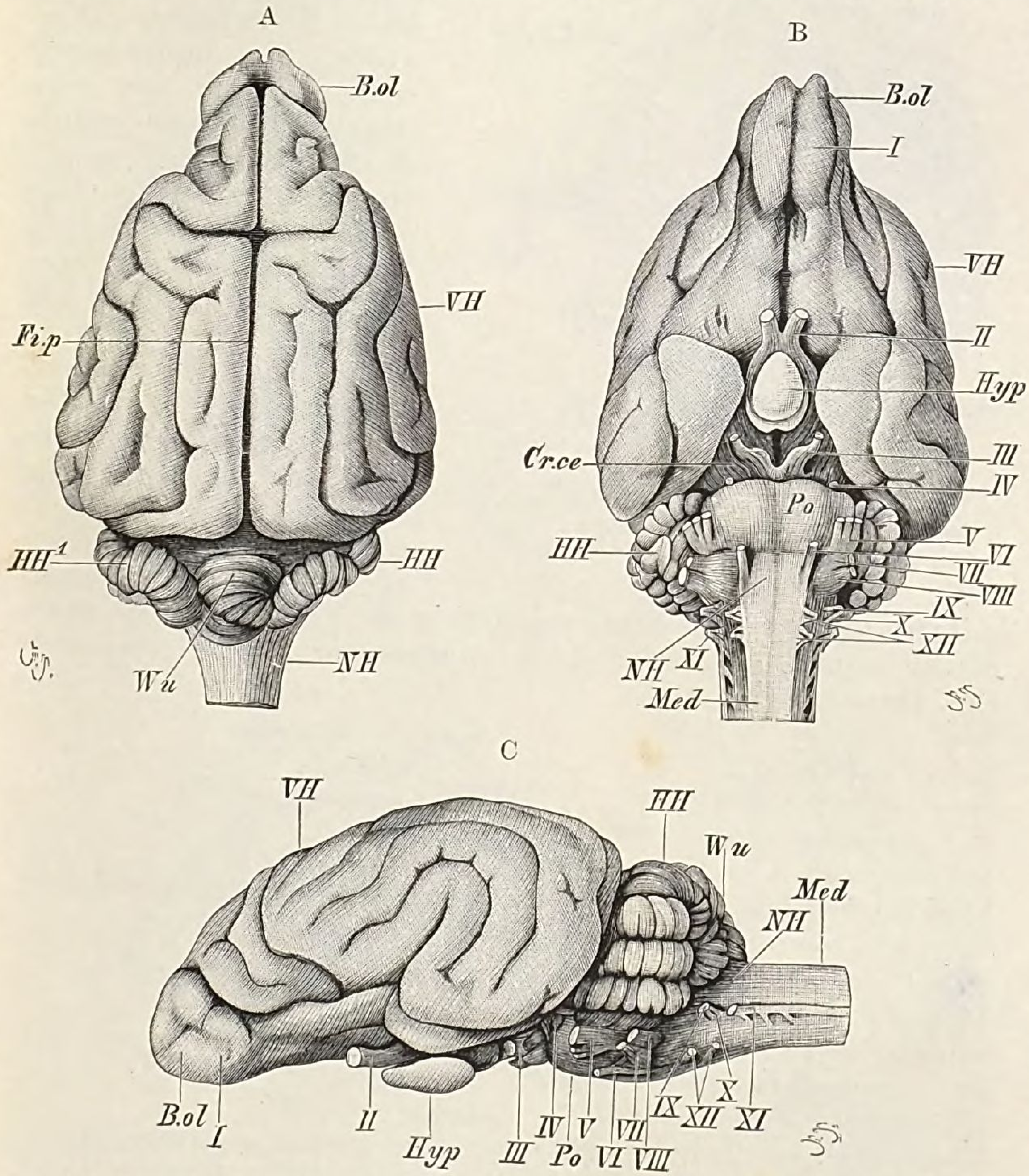


FIG. 1133.—Brain of **Dog.** *A*, dorsal; *B*, ventral; *C*, lateral aspect. *B. ol.* olfactory lobe; *Cr. ce.* crura cerebri; *Fi. p.* great longitudinal fissure; *HH, HH′*, lateral lobes of cerebellum; *Hyp.* hypophysis; *Med.* spinal cord; *NH*, medulla oblongata; *Po.* pons Varolii; *VH.* cerebral hemispheres; *Wu*, middle lobe (vermis) of cerebellum; *I—XII.* cerebral nerves. (From Wiedersheim's *Comparative Anatomy*.)

hippocampal commissure (*hip. com.*), the great development of which readily leads to its being mistaken for a corpus callosum. The fibres entering into the formation of this commissure correspond, however, not to the fibres of the corpus callosum, but, as proved by their

mode of origin, to the fibres of the fornix, and they connect together only the hippocampi, the fasciæ dentatæ, and an area of the hemisphere in front of the anterior commissure (*pre-commissural area*). In the Monotremes (Fig. 1134) the hippocampal commissure is only very slightly bent downwards at its posterior extremity. In most Marsupials (Fig. 1135) it bends sharply round posteriorly and runs forward again, becoming thus folded into two layers, dorsal and ventral, continuous with one another at a posterior bend or *splenium*, similar to the splenium of the corpus callosum. The dorsal layer of the hippocampal commissure becomes completely replaced in the Eutheria by the fibres of the corpus callosum, and the ventral part alone persists in the shape of the lyra.

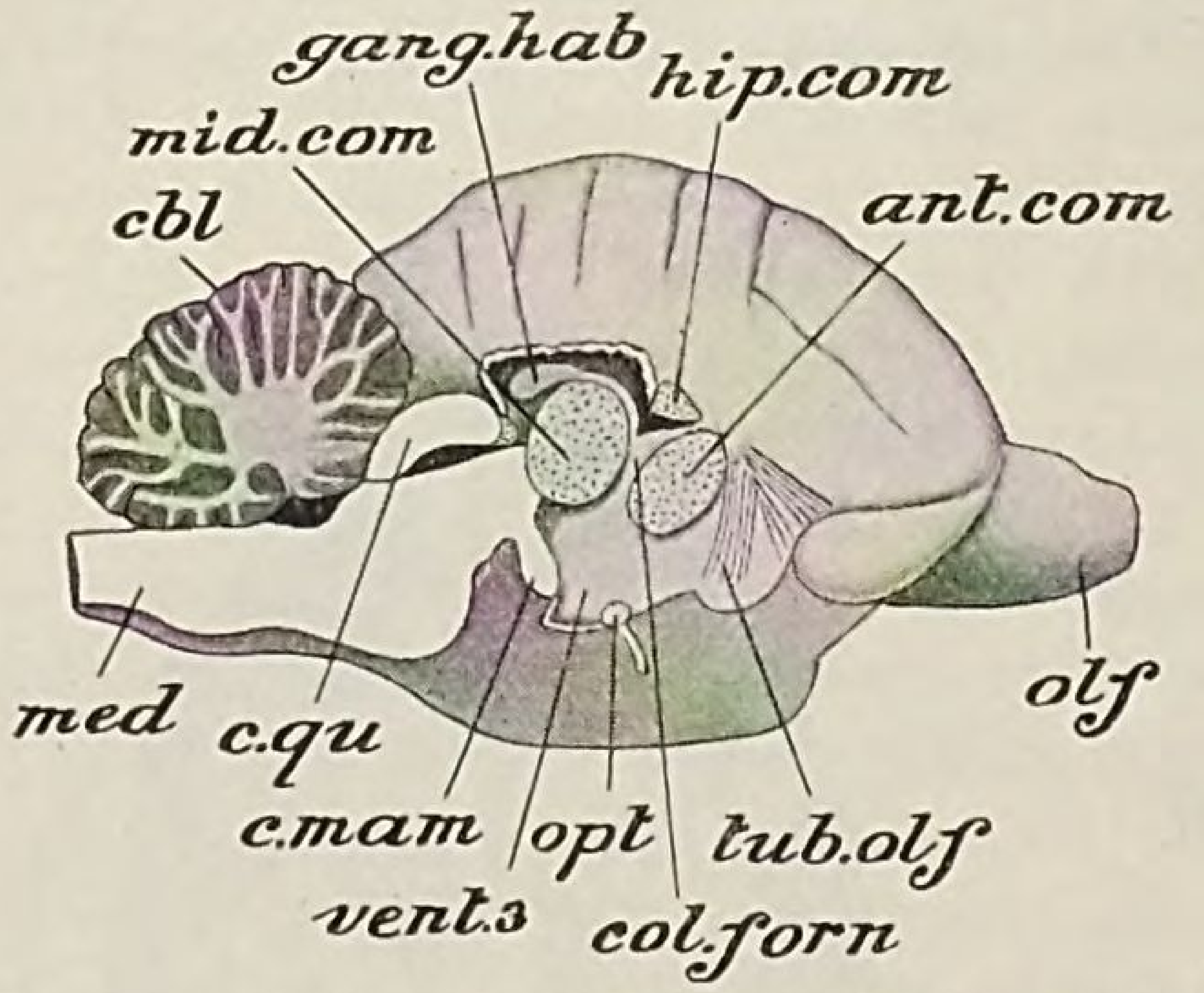


FIG. 1134.—Brain of **Echidna aculeata,** sagittal section. *ant. com.* anterior commissure ; *cbl.* cerebellum ; *c. mam.* corpus mammillare ; *c. qu.* corpora quadrigemina ; *crur.* crura cerebri ; *hip. com.* hippocampal commissure ; *hypo.* hypophysis ; *med.* medulla oblongata ; *mid. com.* middle commissure ; *olf.* olfactory lobe ; *opt.* optic chiasma ; *tub. olf.* tuberculum olfactorium ; *vent.* 3, third ventricle.

In Ornithorhynchus (Fig. 1136) the hemispheres are smooth ; in Echidna (Fig. 1137) they are tolerably richly convoluted. In the lower Marsupials there are no convolutions (Notoryctes, Koala, Phalangers), while in the higher the convolutions are numerous, though the sulci are not very deep (Macropus Fig. 1138). Among the Eutheria there is a great range in the grade of development of the brain, from the Rodents and lower Insectivores to the higher Primates.

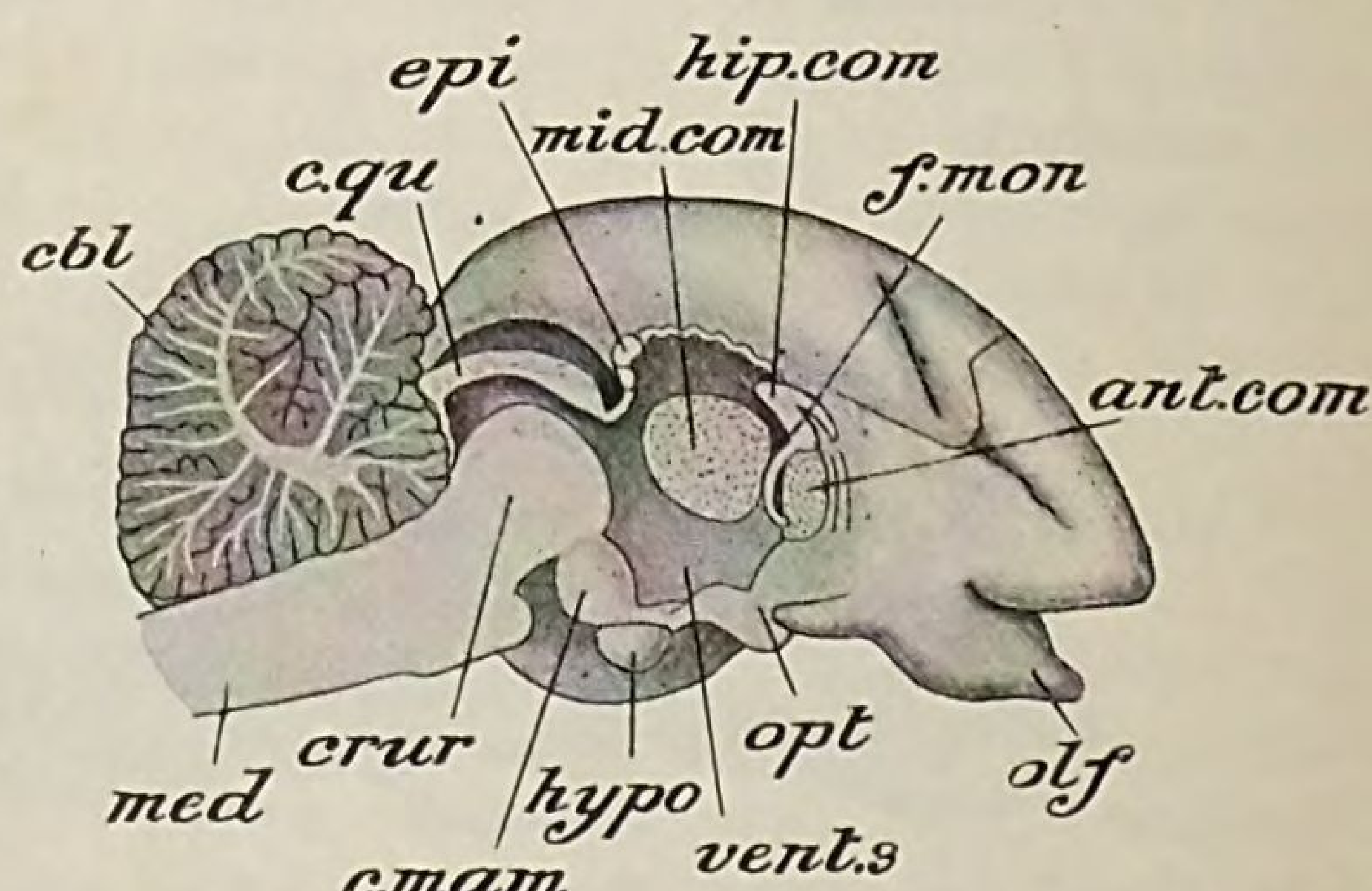


FIG. 1135.—Sagittal section of brain of **Rock Wallaby** (*Petrogale penicillata*). *ant. com.* anterior commissure ; *cbl.* cerebellum ; *c. mam.* corpus mammillare ; *c. qu.* corpora quadrigemina ; *crur.* crura cerebri ; *epi.* epiphysis, with the posterior commissure immediately behind ; *f. Mon.* position of foramen of Monro ; *hip. com.* hippocampal commissure, consisting here of two layers continuous behind at the splenium. somewhat divergent in front where the septum lucidum extends between them ; *hypo.* hypophysis ; *med.* medulla oblongata ; *mid. com.* middle commissure ; *olf.* olfactory lobe ; *opt.* optic chiasma ; *vent.* 3, third ventricle.

In the former the cerebral hemispheres are relatively small, do not overlap the cerebellum, and have smooth, or nearly smooth, surface. In the latter the relative development of the hemispheres is immense, and their backward

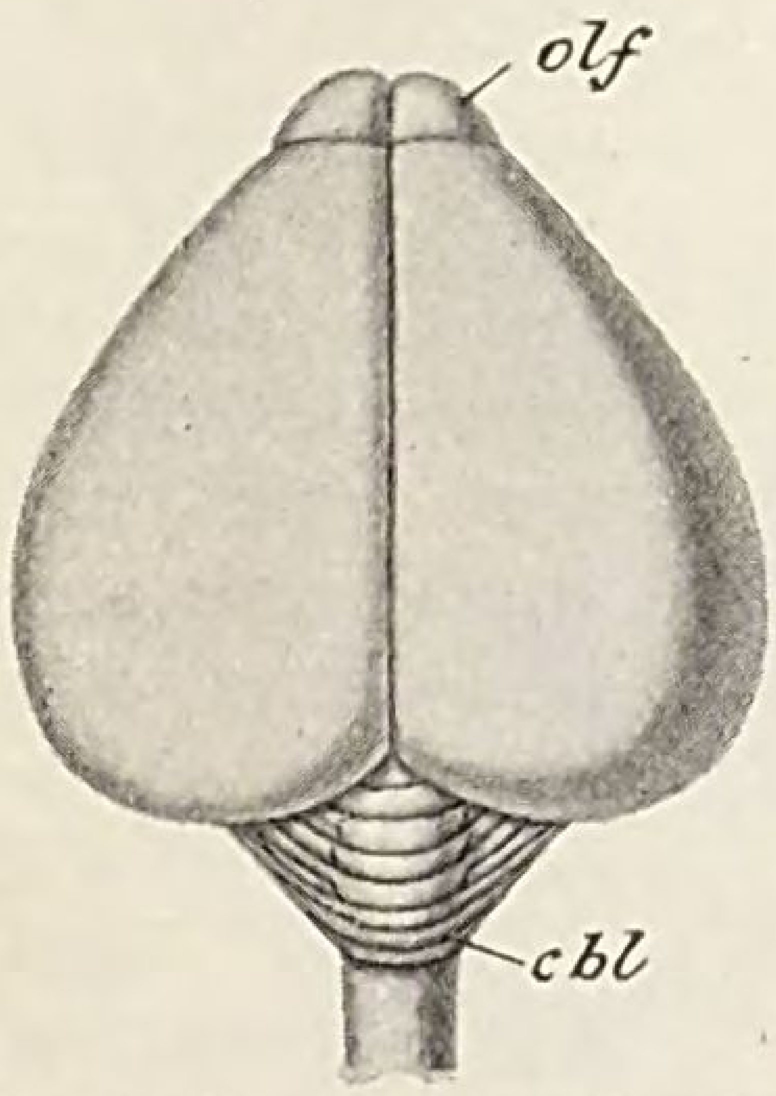


FIG. 1136.—Brain of **Ornithorhynchus anatinus,** dorsal view (natural size); *cbl.* cerebellum; *olf.* olfactory lobes.

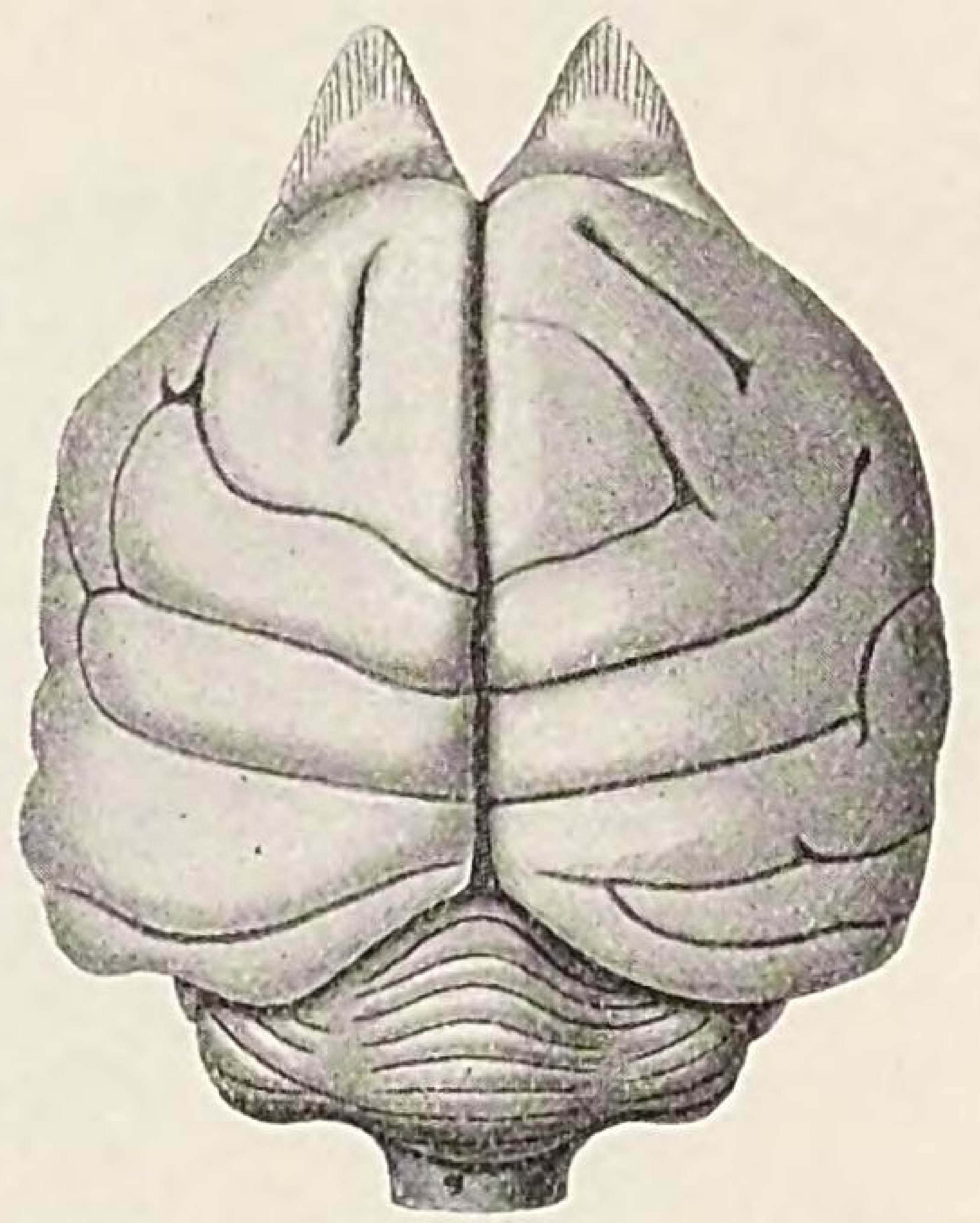


FIG. 1137.—Brain of **Echidna aculeata,** dorsal view (natural size).

extension causes them to cover over all the rest of the brain while the cortex is thrown into numerous complicated convolutions separated by deep sulci (Fig. 1139). This development of the cerebral hemispheres reaches its maximum in Man.

The **organs of special sense** have the same general structure and arrangement as in the Sauropsida. *Jacobson's organs,* which in the Sauropsida constitute such important accessory parts to the olfactory apparatus, are well developed only in the lower groups of Mammals. The *olfactory mucous membrane* is of great extent owing to the development of the convoluted ethmo-turbinal bones over which it extends. In the toothed Cetacea alone among Mammals do the nasal chambers lose their sensory functions—the olfactory nerves being vestigial or absent. The organs of taste are *taste-bulbs* in the mucous membrane covering certain of the papillæ on the surface of the tongue.

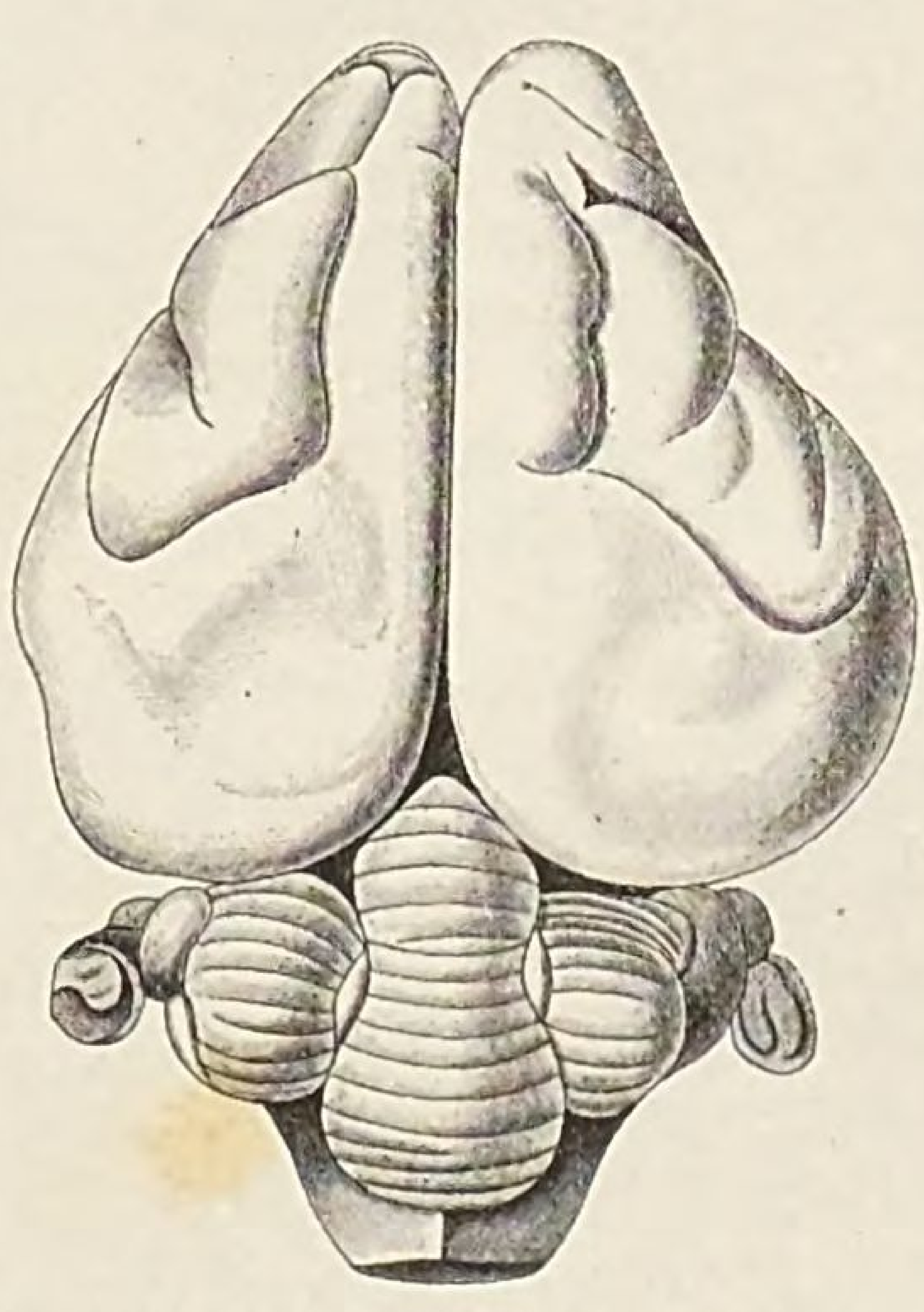


FIG. 1138.—Brain of **Kangaroo** (*Macropus major*). (After Owen.)

In essential structure the *eye* of the Mammal resembles that of the Vertebrates in general (*see* p. 103). The sclerotic is composed of condensed fibrous tissue. The pecten or marsupium of the eye of Birds and Reptiles is absent. In most Mammals there are three movable eyelids, two, upper and lower, opaque and usually covered with hair, and one anterior, translucent, and hairless—the *nictitating membrane*. The secretions of a lacrymal, a Harderian and a series of Meibomian glands moisten and lubricate the surface of the eye-ball and its lids. In Moles, and certain other burrowing Insectivores and Rodents, and in Notoryctes among the Marsupials, the eyes are imperfectly developed and functionless.

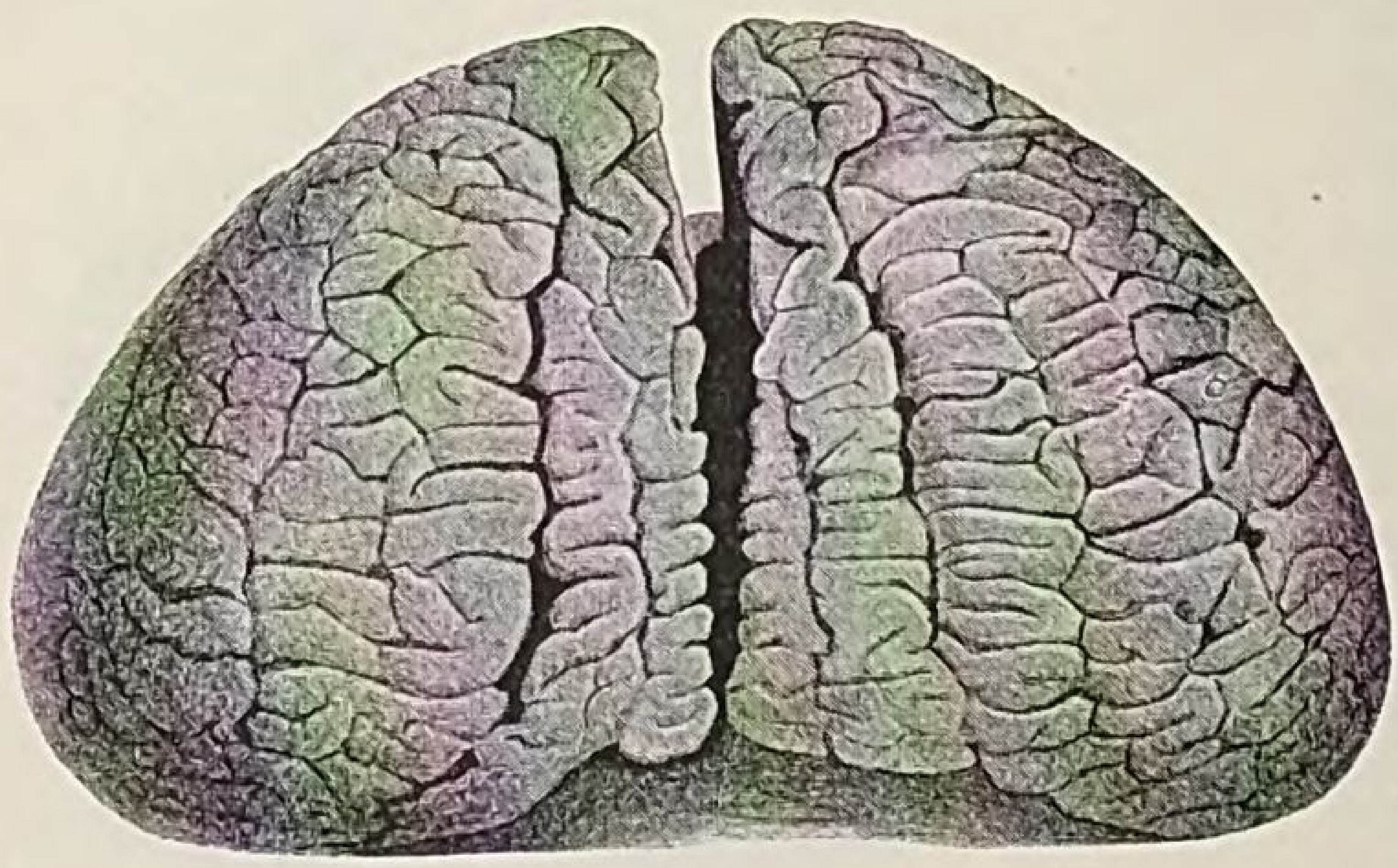


FIG. 1139.—Dorsal view of brain of **Gray's Whale** (*Cogia grayi*). (After Haswell.)

The *ear* of a Mammal is more highly developed than that of other Vertebrates, both in respect of the greater complexity of the essential part—the membranous labyrinth—and in the greater development of the accessory parts. A large external *auditory pinna*, supported by cartilage, is almost invariably present, except in the Monotremata, Cetacea, and Sirenia. This is a widely open funnel, of a variety of shapes in different groups, having the function of collecting the waves of sound. By the action of a system of muscles it is capable of being turned about in different directions. Enclosed by its basal part is the opening of the *external auditory passage* (Fig. 1141, *Ex.*). This, the length of which varies, leads in-

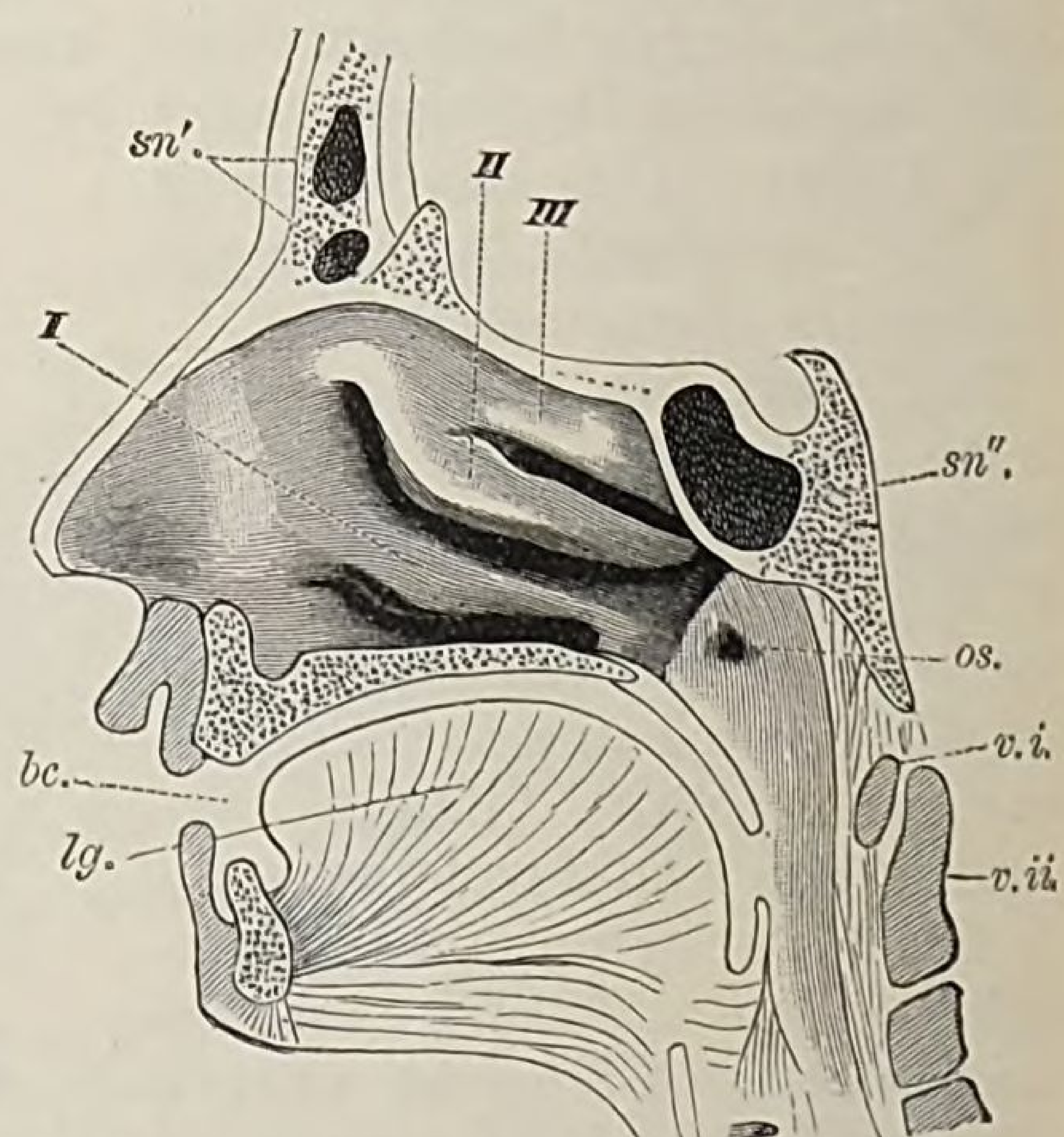


FIG. 1140.—Sagittal section through the nasal and buccal cavities of the human head. *I*, *II*, *III*, the three olfactory ridges formed by the turbinals; *bc*, entrance to the mouth; *lg.* tongue; *os*, opening of Eustachian tube; *sn'*, frontal sinus; *sn''*, sphenoidal sinus; *v. i*, atlas vertebra; *v. ii*, axis vertebra. (After Wiedersheim.)

wards to the *tympanic membrane* (*M.*), which separates it from the cavity of the middle ear or *tympanic cavity*. The wall of the external auditory passage is sometimes entirely membranous or cartilaginous, sometimes in part supported by a tubular part of the tympanic bone; in Echidna it is strengthened by a series of incomplete rings of cartilage. The tympanic cavity, enclosed by the periotic and tympanic bones, communicates with the upper or respiratory division of the pharynx by a longer or shorter tubular passage—the *Eustachian tube* (*E.*). On its inner wall are the *fenestræ ovalis* and *rotunda*, and across its cavity, from the tympanic membrane to the fenestra ovalis, runs the irregular chain of auditory

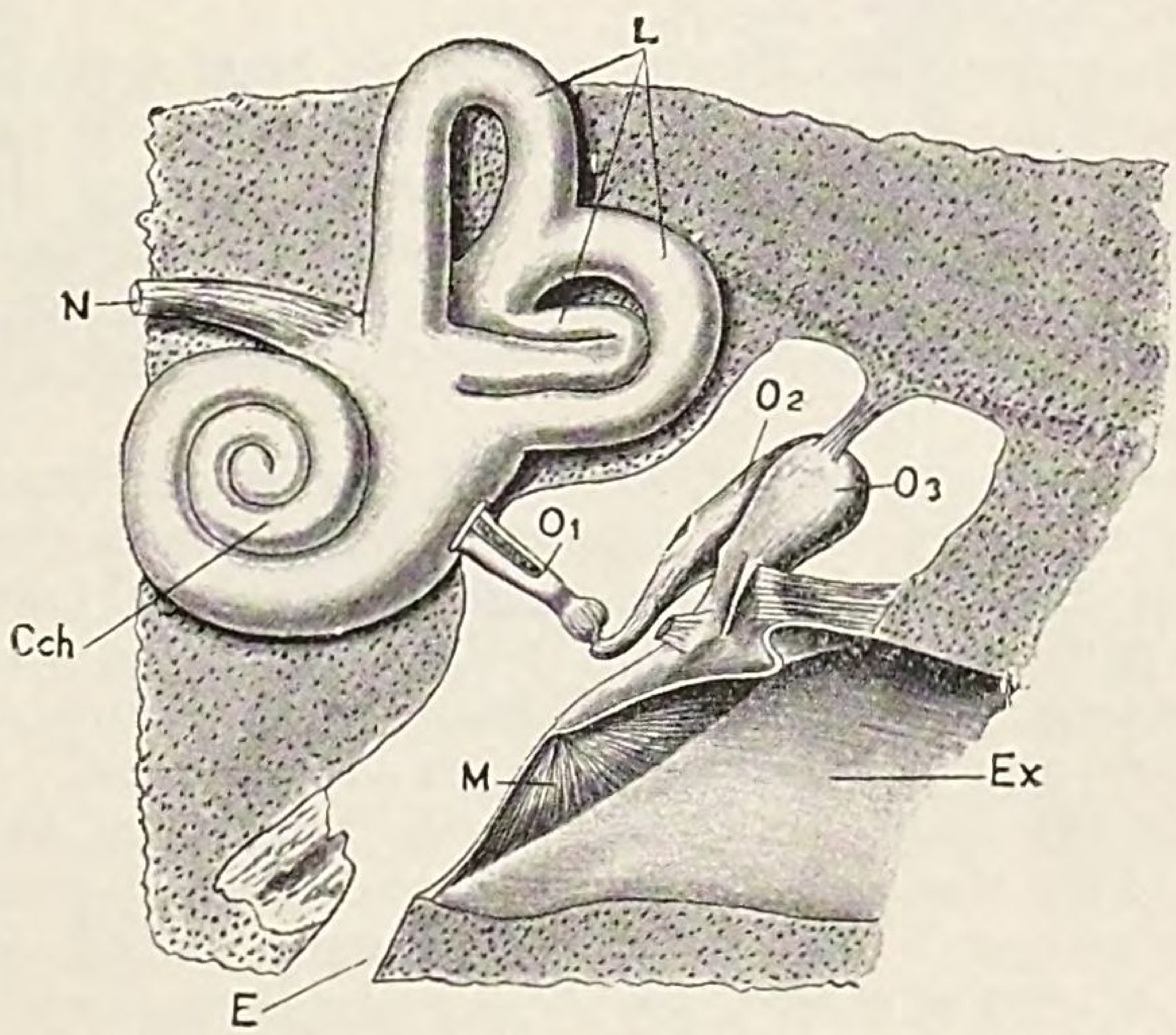


FIG. 1141.—Parts of the **Human ear** (diagrammatic). *Cch.* cochlea; *E.* Eustachian tube; *Ex.* outer opening of ear; *L.* labyrinth; *M.* tympanic membrane; *N.* entrance of auditory nerve; O_1. O_2. O_3. the three auditory ossicles, stapes, incus, malleus. (After Headley.)

ossicles—the malleus (O_3.), the incus (O_2.), and the stapes (O_1.). These vary somewhat in form in different Mammals. The stapes is usually perforated by a considerable foramen, as in the Rabbit; but, in the Monotremes and Marsupials, approximates more towards the rod-like shape which the columella presents in Amphibia, Reptiles, and Birds. The *membranous labyrinth* (*L.*) of the internal ear of a Mammal is characterised by the special development of the *cochlea* (*Cch.*), which (except in the Monotremes) is coiled into a spiral like the shell of a Helix.

Urinogenital Organs.—The *kidneys* of Mammals are compact organs of oval shape. On the inner side is a notch or *hilus*, by which vessels and ducts enter or leave the interior of the kidney. The substance of the kidney consists of two distinctly marked portions—a central portion or *medulla*, and an outer part or *cortex;* the former is the secreting part, the latter consists of a mass of

straight tubules by which the secretion is carried to the ureter. The ureter dilates as it enters the kidneys to form a chamber—the *pelvis*—into which the straight tubules of the medulla of the kidney open. The openings of the tubules are on the summits of papillæ, which are the apices of a series of pyramidal masses into which, in most cases, the substance of the kidney is incompletely divided. In many Mammals, however (some Primates, the Carnivora, and Rodentia), there is no such division of the kidney substance, and all the ducts open on the surface of a single papilla. In other Mammals again (Ox, Bears, Seals, Cetacea) the division carried so far that the kidney is divided externally into a number of distinctly separated lobules.

The ureters in all the Theria open into a large median sac—the *urinary bladder*—situated in the posterior or pelvic part of the cavity of the abdomen. From this a median passage, the *urethra*—into which in the male the *vasa deferentia* open—leads to the exterior. Only in the Monotremes do the two ureters and the bladder all have separate openings into the urinogenital division of the cloaca.

The testes are oval bodies, which only exceptionally retain their original position in the abdominal cavity, descending in the majority of Mammals through a canal—the *inguinal canal*—in the posterior part of the abdominal wall to lie in the *perinæum*, or space between the urinogenital and anal apertures, or to be received into a pendulous pouch of skin—the *scrotum*. The *penis*, present in the males of all Mammalia, consists of two *corpora cavernosa*, firm strands of vascular tissue attached proximally to the ischia except in the Monotremes, Marsupials and some Edentata, and a central strand, the *corpus spongiosum*, perforated by the urethral canal and dilated at the extremity to form the *glans*. The two *vasa deferentia*, continued from the epididymes, which are in close relation to the testes, join the urethral canal near the neck of the bladder, each having connected with it, near its distal end, a sacculated reservoir —the *vesicula seminalis*. A small diverticulum of the proximal part of the urethra—the *uterus masculinus*—appears to be a remnant of the Müllerian duct. Surrounding this part of the urethra is a glandular mass—the *prostate gland*; and the ducts of a pair of small glands—*Cowper's glands*—open into the urethra near the base of the penis.

The *ovaries* are compressed oval bodies which retain their primary position in the abdomen, or pass backwards into its posterior or pelvic part. In the Monotremes large Graafian follicles project on the surface of the ovary, while in other Mammals the Graafian follicles are very small, and the surface of the ovary almost smooth.

The *oviducts* have dilated funnel-like abdominal openings, the edges of which, except in the Monotremes, are fimbriated or

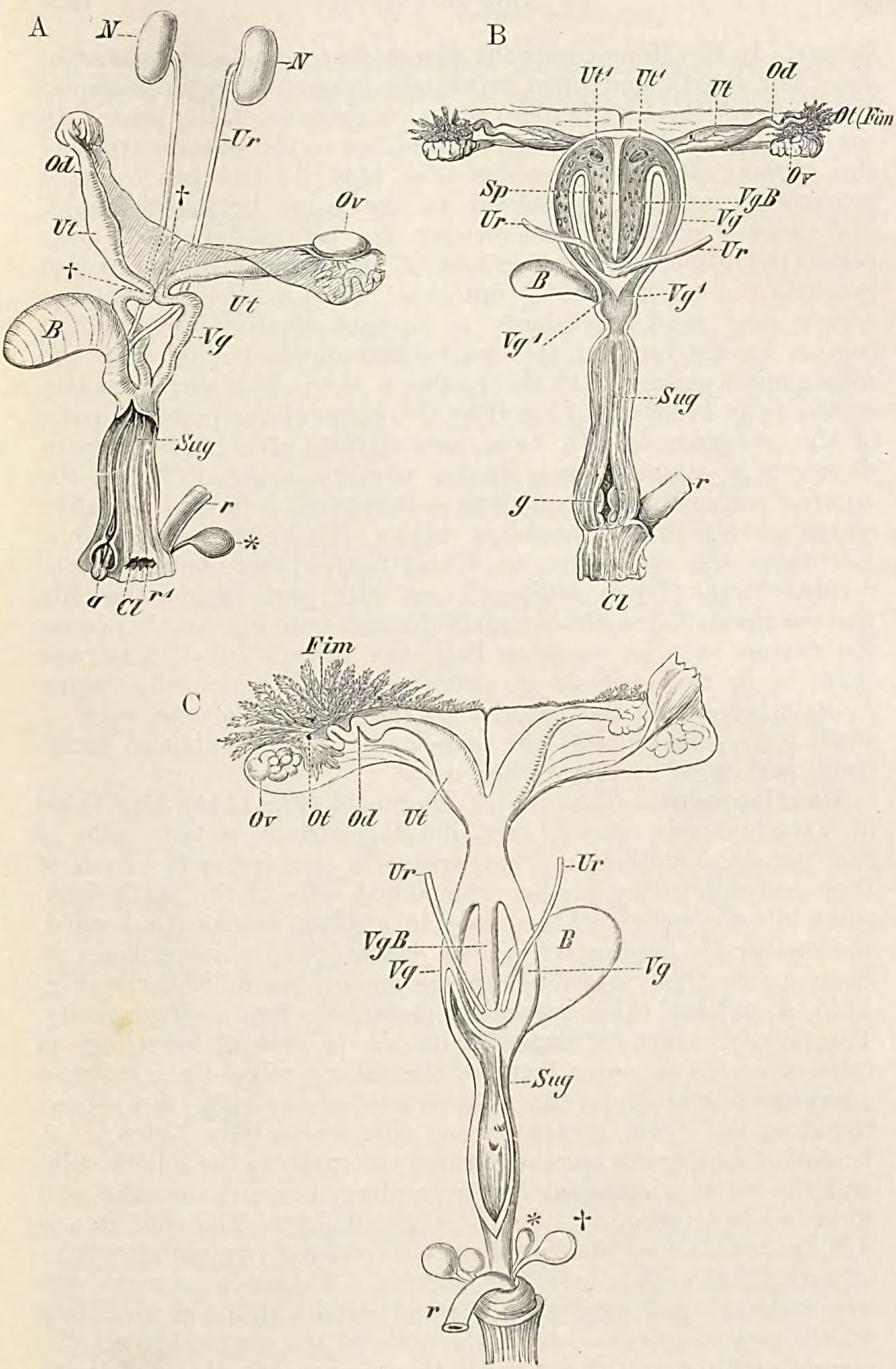


FIG. 1142.—Female urinogenital apparatus of various **Marsupials.** A, **Didelphys dorsigera** (young); B, **Trichosurus;** C, **Phascolomys wombat.** *B*, urinary bladder; *Cl.* "cloaca"; *Fm.* fimbriæ; *g.* clitoris; *N*, kidney; *Ot.* aperture of Fallopian tube; *Ov.* ovary; *r.* rectum; *Ur.* ureter; *Ut.* uterus; *Ut'.* opening of the uterus into the median vagina (*Vg.B.*); *Vg.* lateral vagina; *Vg'.* its opening into the urinogenital sinus; † *, rectal glands. (From Wiedersheim's *Comparative Anatomy.*

fringed. In the Monotremes the two oviducts are distinct throughout their length, and open separately into a urinogenital sinus. In nearly all the Theria more or less coalescence takes place. In the Marsupials this coalescence is confined to the anterior part of the vagina. In the Opossums (Fig. 1142, A) the two oviducts are merely in close apposition at one point behind the uteri, and there is no actual coalescence. In the rest of the Marsupials (B, C) the anterior portions of the oviduct in the region (vagina) behind the uteri unite to form a median chamber which may send backwards a median diverticulum (*median vagina, Vg.* B), and in this way communicate behind with the urinogenital passage. In the Eutheria there is a single median *vagina* (Fig. 1143, *Vg.*) formed by the union of the posterior parts of the two oviducts. In some cases the two uteri (A, *ut.*) remain distinct; in others their posterior portions coalesce (B, C), the anterior parts remaining separate so that there is formed a median *corpus uteri* with two horns or *cornua*. In Primates and some Edentates the coalescence goes still further, there being an undivided uterus (D) in addition to an undivided vagina, the only parts of the oviducts which remain distinct from one another being the narrow anterior parts or Fallopian tubes. In all Mammals there is, in the *vestibule* or passage through which the vagina communicates with the exterior by the aperture of the *vulva*, a small body—the *clitoris*—the homologue of the penis and sometimes perforated by the urethral canal.

Development.—The ova of Mammals (Fig. 1144), like those of Vertebrates in general, are developed from certain cells of the germinal epithelium, the *primitive ova* (*pr. ov.*). Each of these, surrounded by smaller unmodified cells of the epithelium, sinks into the stroma of the ovary, in which it becomes imbedded, the small cells forming a *Graafian follicle* (*foll.*) which encloses it. Soon spaces filled with fluid appear among the follicle cells (Fig. 1145, A, *sp.*), and these eventually coalesce to form a single cavity. This cavity, which in some Mammals is crossed by strings of cells, separates an outer layer of the follicle cells—the *membrana granulosa* (*mem.*)—from the mass—*cumulus proligerus* (*disc.*)—surrounding the ovum, except on one side where they coalesce. A basement membrane becomes formed externally to the follicle cells, and the stroma, immediately surrounding, becomes vascular, and forms a two-layered investment for the follicle. The cells immediately surrounding the ovum become arranged as a definite layer of cylindrical cells—the *corona radiata*. A thick membrane—the *zona radiata*—perforated by numerous radially arranged pores, into which project processes from the cells of the corona, invests the ovum; and in many, if not in all, there is beneath this a delicate vitelline membrane. As the ovum increases in size, granules of yolk become distinguishable among the protoplasm.

As the ovum approaches maturity the fluid—*liquor folliculi*—in the cavity of the follicle increases in quantity, so that the follicle

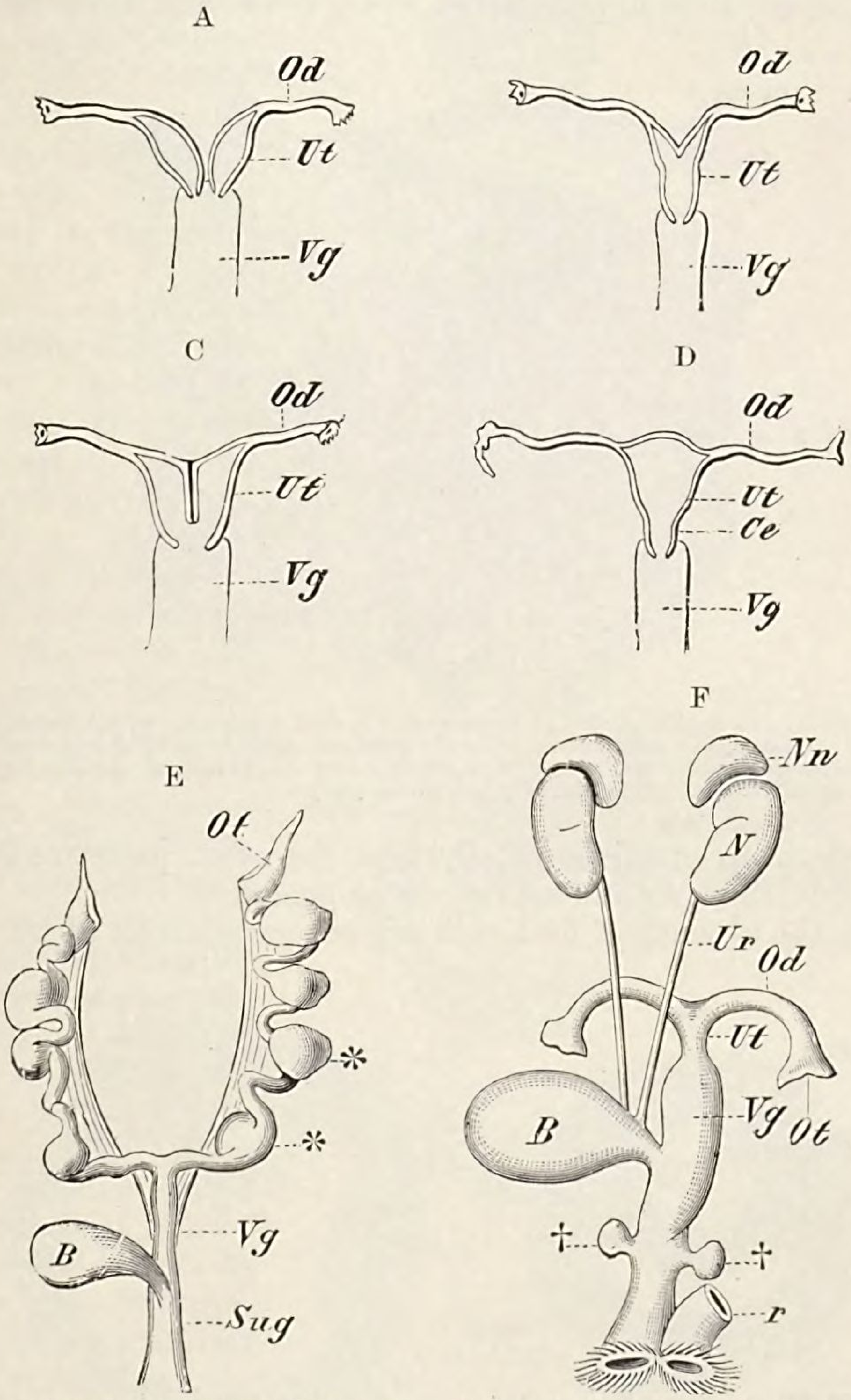


FIG. 1143.—Various forms of uteri in **Eutheria.** A, B, C, D, diagrams illustrating the different degrees of coalescence of the oviducts. A, two distinct uteri. B, bicornuate uterus. C, uterus with a median partition. D, complete coalescence. E, female reproductive organs of one of the *Mustelina* with embryos (* *) in the uterus. F, female reproductive organs of the Hedgehog. *B*, urinary bladder; *Ce.* cervix uteri (neck of uterus); *N*, *Nn*, kidneys and adrenal bodies; *Od.* oviduct; *Ot.* ostium tubæ (abdominal opening of oviduct); *Sug.* urino-genital sinus; *r.* rectum; *Ur.* ureters; *Ut.* uterus; *Vg.* vagina; † †, accessory glands. (From Wiedersheim's *Comparative Anatomy*.)

becomes greatly distended. The follicle has, meanwhile, approached the surface of the ovary, on which it comes to project as a rounded prominence. Eventually the middle region of the projecting part

of the wall of the follicle thins out and ruptures, setting free the ovum which passes into the Fallopian tube. On the way along the Fallopian tube impregnation takes place, and, after becoming

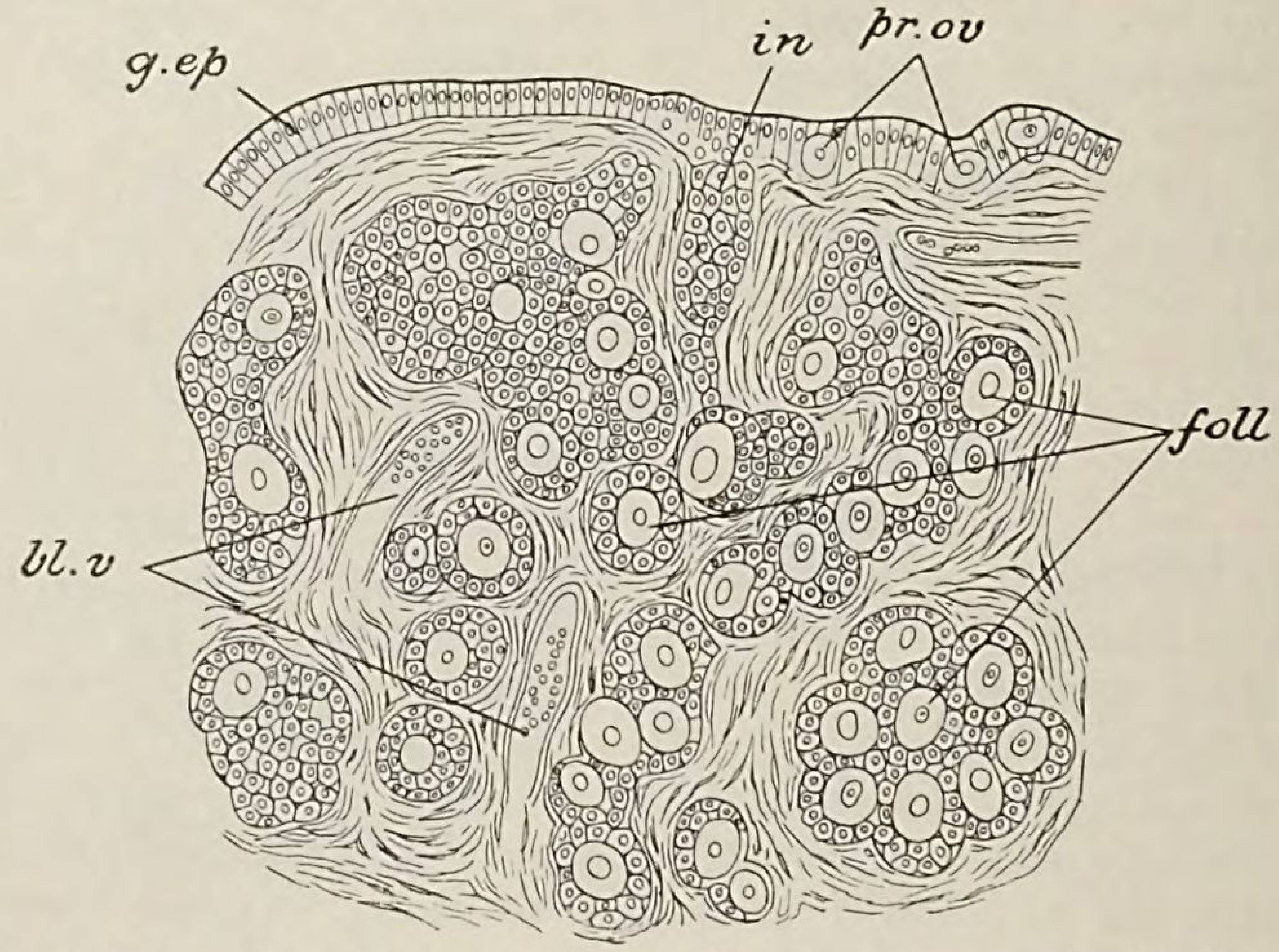


FIG. 1144.—Part of a sagittal section of an **ovary** of a child just born. *bl. v.* blood-vessels ; *foll.* strings and groups of cells derived from the germinal epithelium becoming developed into follicles ; *g. ep.* germinal epithelium ; *in.* ingrowing cord of cells from the germinal epithelium ; *pr. ov.* primitive ova. (From Hertwig, after Waldeyer.)

enclosed in an envelope of albumen, the ovum passes onwards to the uterus, there to undergo its development.

With the absence of food-yolk are connected most of the differ-

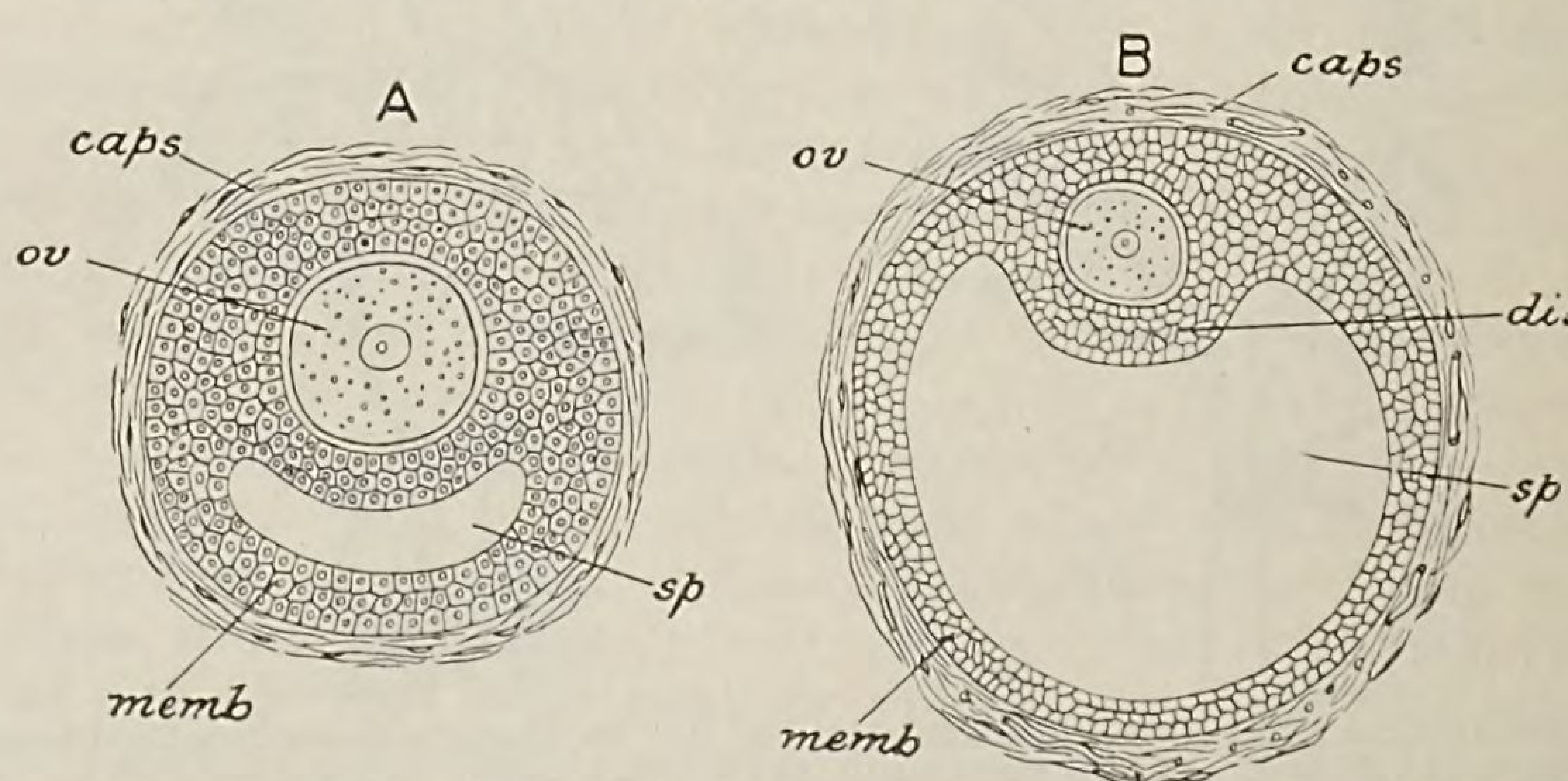


FIG. 1145.—Two stages in the development of the **Graafian follicle.** *A*, with the follicular fluid beginning to appear ; *B*, after the space has largely increased ; *caps.* capsule ; *disc.* cumulus proligerus ; *mem.* membrana granulosa ; *ov.* ovum ; *sp.* space containing fluid. (After Hertwig.)

ences observable between the early stages of the development of a Mammal (Fig. 1146), and the corresponding stages in the development of a Reptile or Bird. One of the most striking of these is in the mode of segmentation. In the case of the large ovum of the Bird, as

we have seen, the segmentation is of the incomplete, or *meroblastic* type, being confined to a small disc of protoplasm—the *germinal disc*—on one side of the ovum. In the Mammal, on the other hand, except in the Monotremes and some Marsupials, segmentation is complete or *holoblastic*, the entire ovum taking part in the process of segmentation. The segmentation is very irregular, the cells into which the ovum divides being of unequal size. The result is the formation of a sphere of cells, which soon become distinguishable into an outer layer and a central mass, the *embryonic cell-mass.* By imbibition of liquid a cavity, which is formed in the interior of the ovum, increases rapidly in size. The stage now reached is called the *blastodermic vesicle.* During the growth in size of the internal cavity the central mass of cells remains in contact with one side only of the outer layer, where it spreads out as a stratum several cells deep. It is in this region—the *embryonic area*—that the first rudiments of the embryo become developed.

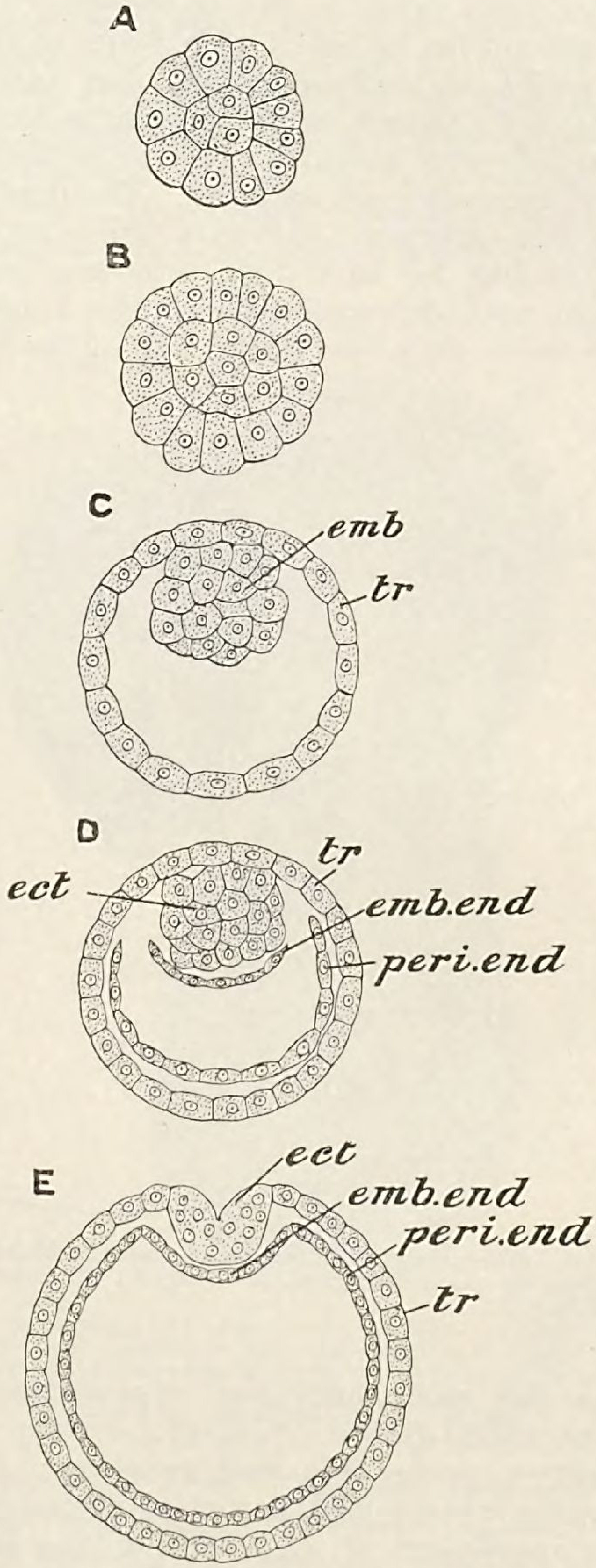


FIG. 1146.—Diagram representing sections of the embryo of a **Mammal** at successive stages in the segmentation and formation of the layers. *A* and *B*, formation of enclosing layer (trophoblast) and central cell-mass destined to give rise to the embryo; *C*, blastodermic vesicle with embryonic cell-mass separated from trophoblast except on one side; *D*, blastodermic vesicle in which peripheral and embryonic portions of endoderm have become established; *E*, stage in which the embryonic ectoderm has broken through the trophoblast and become joined to it peripherally, and in which the embryonic and peripheral endoderm have also become continuous.

The outer layer is the *trophoblast.* Immediately beneath it, throughout its extent, a thin layer of flattened cells appears—the *peripheral endoderm*—and this becomes continuous with a similar layer formed on the inner surface of the embryonic cell-mass—the *embryonic endoderm.* The rest of the embryonic cell-mass gives rise to the *embryonic ectoderm.* The part of the trophoblast lying over this embryonic ectoderm thins out and disappears, or fuses with it, and the embryonic ectoderm becomes continuous at its margin with the remainder of the trophoblast, which forms the outer layer of the rest of the wall of the blastodermic vesicle.

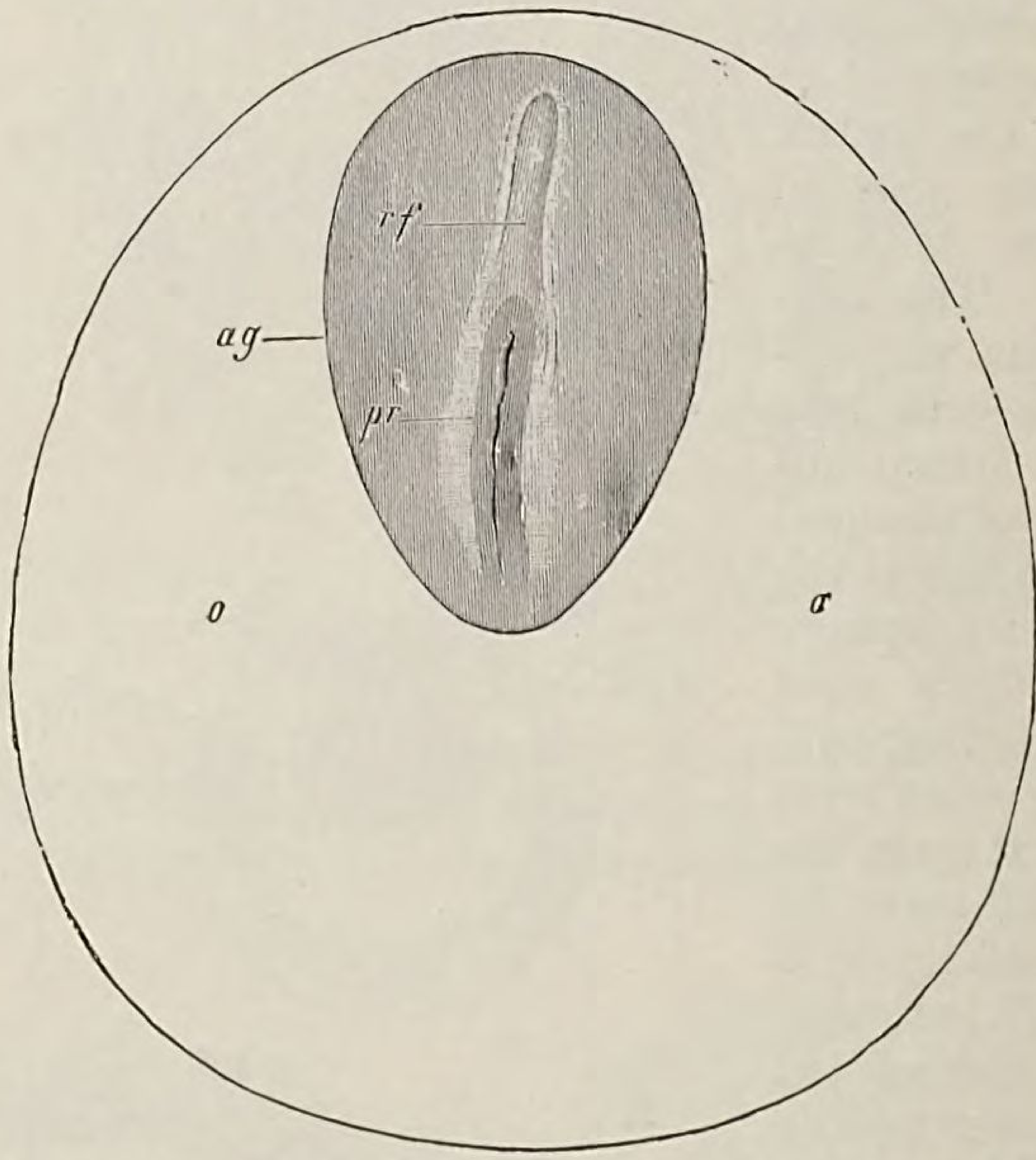


FIG. 1147.—Embryonic area of a seven days' **embryo Rabbit.** *ag*, embryonic area; *o*, place of future vascular area; *pr.* primitive streak; *rf*, medullary groove. (From Balfour after Kölliker.)

On the embryonic area a *primitive streak* (Fig. 1147, *pr.*) and primitive groove are developed very much as in the Bird. A *medullary groove* (*rf*) and *canal* are formed in front of the primitive groove, and a row of protovertebræ (Fig. 1148) make their appearance on each side of the former. The embryo becomes folded off from the blastoderm as in the Bird, and at length the body of the young Mammal becomes constricted off from the yolk-sac or *umbilical vesicle*, so that, ultimately, the two come to be connected only by a narrow yolk-stalk (Figs. 1149 and 1150): the yolk-sac is a thin-walled sac containing a coagulable fluid in place of yolk. A *vascular area* early becomes established around the embryo on the wall of the yolk-sac.

The most important of the points of difference between a Mammal and a Bird, as regards the later part of the history of the development, are connected with the fate of the *fœtal membranes.* The amnion is in many Mammals developed in the same way as in the Bird, viz.: by the formation of a system of folds which arise from the blastoderm around the embryo, and grow upwards and inwards, eventually meeting in the middle over the body of the embryo, and uniting in such a way as to form two layers. Of the

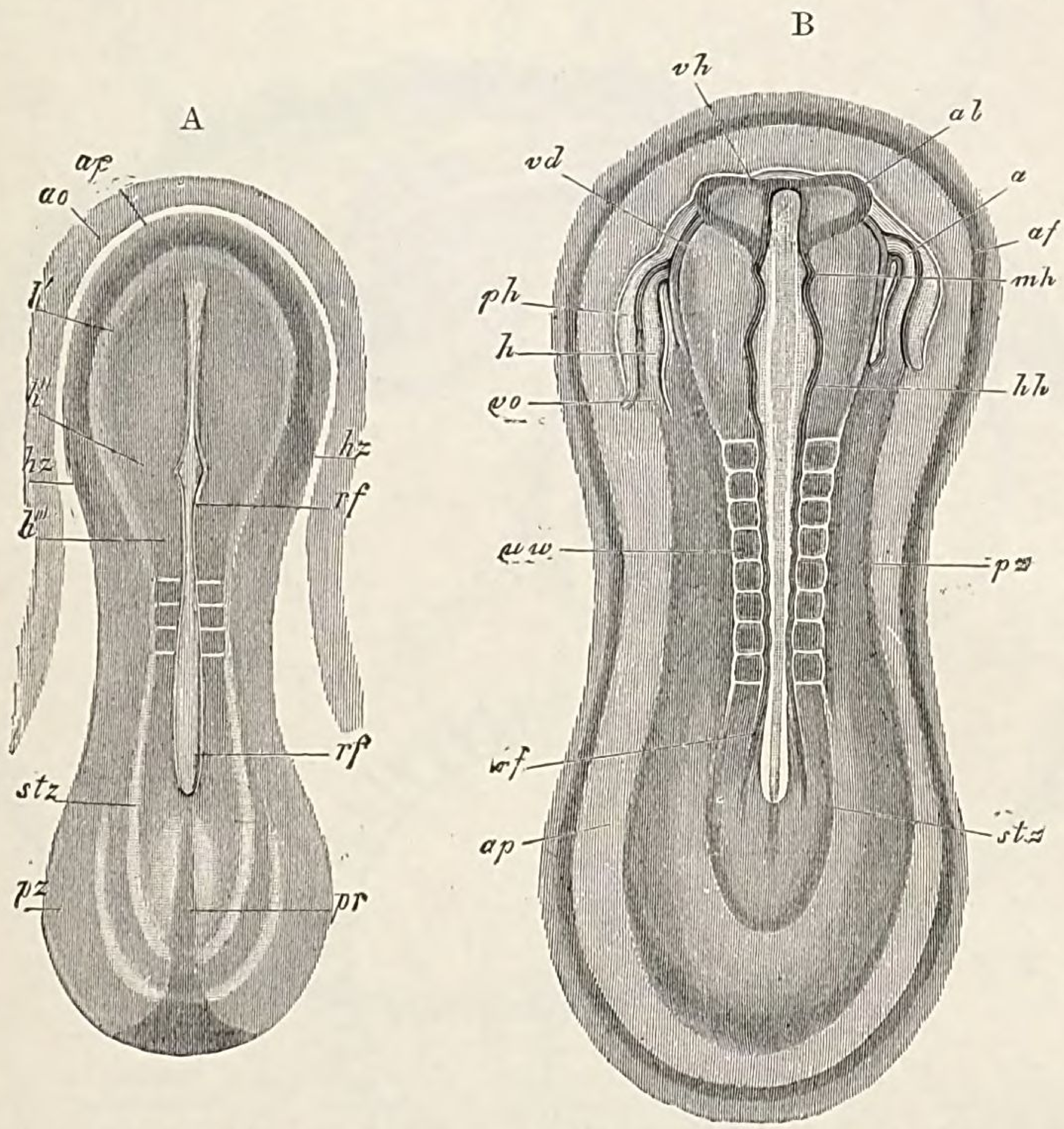


FIG. 1148.—**Embryo Rabbit**, of about nine days, from the dorsal side. *ab*, optic vesicle; *af.* fold of amnion; *op.* area pellucida; *h.* heart; *h'*, medullary plate in the region of the future fore-brain; *h''*, medullary plate in the region of the future mid-brain; *hh*, and *h'''*, hind-brain; *mh*, mid-brain; *ph*, pericardial section of body cavity; *pz*, lateral zone; *rf.* medullary groove; *stz*, vertebral zone; *vo*, vitelline vein. (From Balfour, after Kölliker.)

two layers thus formed the outer (Fig. 1149, 2 and 3) is, from its mode of formation, continuous with the trophoblast which invests the yolk-sac and its stalk, and with it forms a complete investment for the entire ovum: in the account of the development of the Bird it has been referred to as the *serous membrane.* The inner layer or amnion, as in the Bird, forms the wall of a cavity —the *amniotic cavity* (4 and 5, *ah*)—which becomes tensely filled with fluid (the *liquor amnii*) over the body of the embryo; this serves the purpose of protecting the delicate embryo from

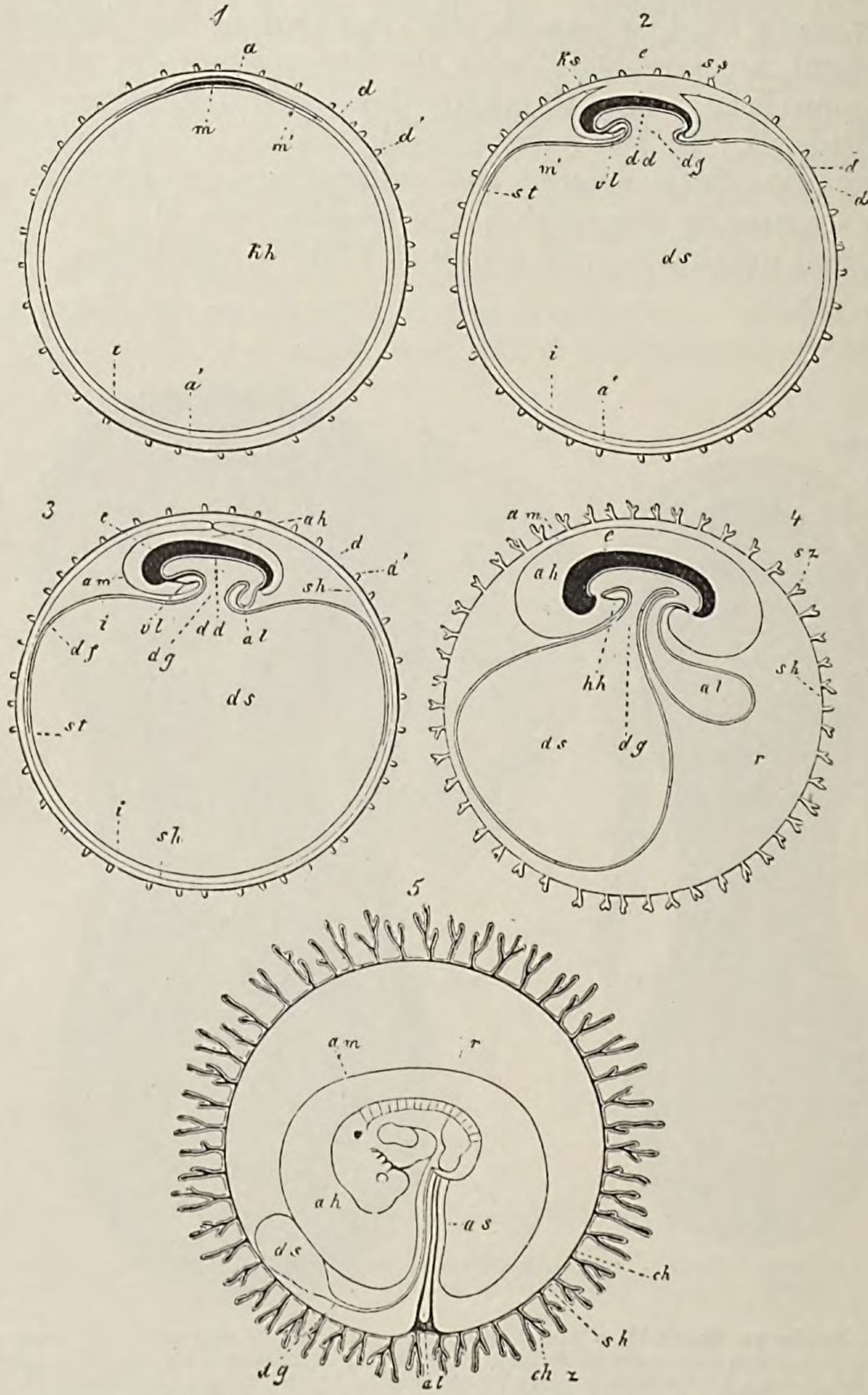


FIG. 1149.—Five diagrammatic sections illustrating the formation of the **fœtal membranes** of a Mammal. In 1, 2, 3, 4 the embryo is represented in longitudinal section. 1, Ovum with zona pellucida, blastodermic vesicle, and embryonic area; 2, ovum with commencing formation of umbilical vesicle and amnion; 3, ovum with amnion about to close; 4, ovum with villous subzonal membrane, larger allantois, and mouth and anus; 5, ovum in which the mesoderm of the allantois has extended round the inner surface of the subzonal membrane and united with it to form the chorion; the cavity of the allantois is aborted; *a*, ectoderm of embryo; *a'*, ectoderm of non-embryonic part of the blastodermic vesicle; *ah.* amniotic cavity; *al.* allantois; *am.* amnion; *ch.* chorion; *chz*, chorionic villi; *d*, zona radiata; *d'.* processes of zona; *dd*, embryonic endoderm; *df.* area vasculosa; *dg*, stalk of umbilical vesicle; *ds*, cavity of umbilical vesicle; *e.* embryo; *hh*, pericardial cavity; *i*, non-embryonic endoderm; *Kh*, cavity of blastodermic vesicle; *Ks.* head-fold of amnion; *m.* embryonic mesoderm; *m'.* non-embryonic mesoderm; *r*, space between chorion and amnion; *sh*, subzonal membrane; *ss*, tail-fold of amnion; *st*, sinus terminalis; *vl.* ventral body wall (From Balfour, after Kölliker.)

the effects of shocks. As in the case of the Bird, the folds giving rise to the amnion and serous membrane, may consist from the first (except the head-fold which, being formed from the proamnion, consists solely of ectoderm) of somatic mesoderm as well as ectoderm; or mesoderm may extend into them later, so that, either from the first, or as a result of outgrowth which takes place subsequently, the serous membrane may contain mesoderm as well as ectoderm, but in some Mammals it appears

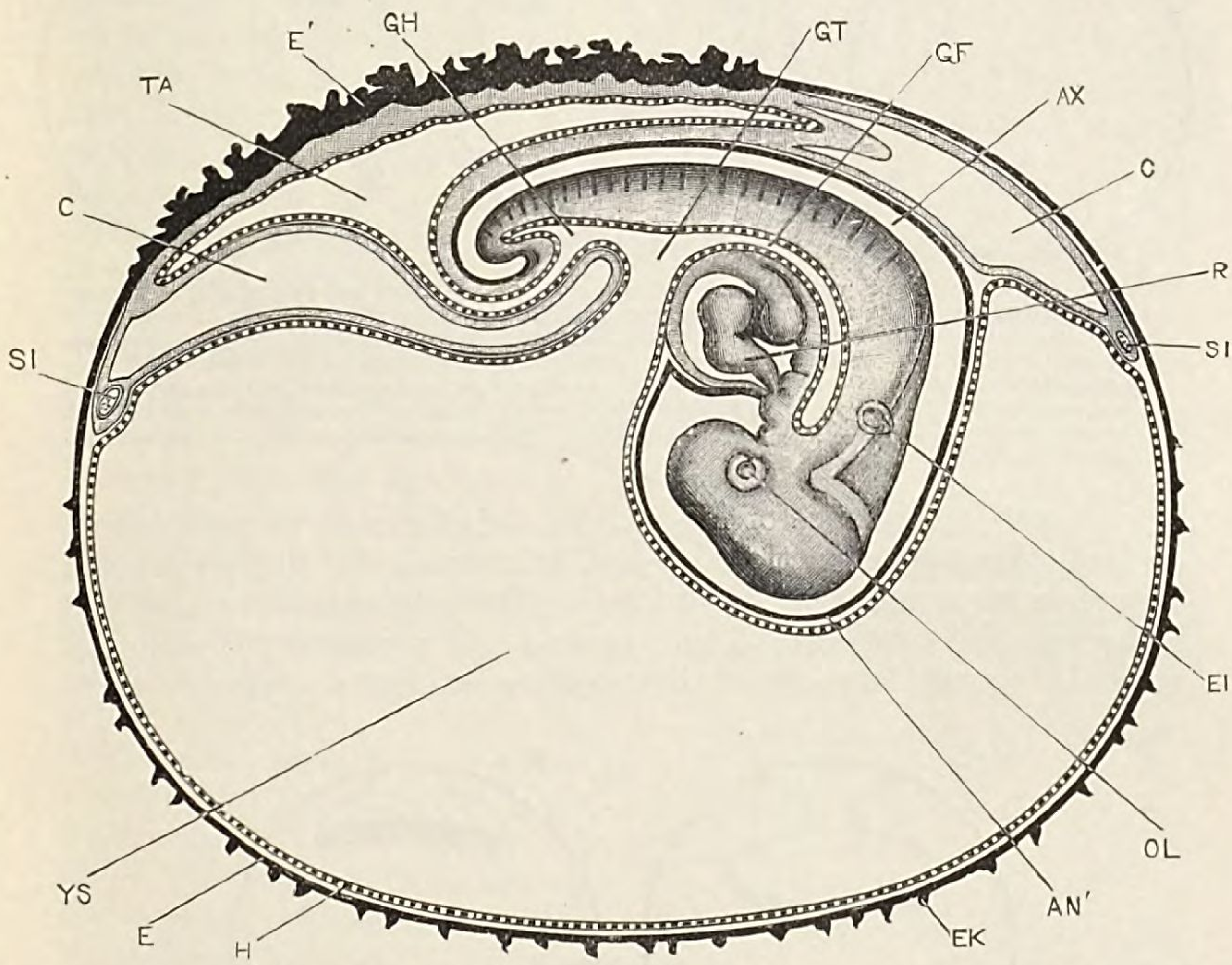


FIG. 1150.—A **Rabbit** embryo and blastodermic vesicle at the end of the tenth day. The embryo is represented in surface view from the right side, the course of the alimentary canal being indicated by the broad dotted line; the blastodermic vesicle is shown in median longitudinal section. The greater part of the tail has been removed. *AN'*. pro-amnion; *AX*. cavity of amnion; *C*. extra-embryonic portion of cœlome; *E*. ectoderm; *E'*. thickened ectoderm by which the vesicle is attached to the uterus and from which the fœtal part of the placental is derived; *EGT*. ectodermal villi; *EI*. auditory vesicle; *GF*. fore-gut; *GH*. hind-gut; *GT*. mid-gut; *H*. endoderm; *OL*. lens of eye; *R*. heart; *SI*. sinus-terminalis; *TA*. allantoic cavity; *YS*. yolk-sac. (From Marshall, in part after Van Beneden and Julin.)

to remain entirely ectodermal. The ectodermal cells—trophoblast cells—of the serous membrane enter into close relationship with the mucous membrane of the wall of the uterus, and send out processes or *villi*, by means of which the ovum becomes intimately attached, and by means of which nourishment is absorbed.

A study of the development of the amnion in various Mammals appears to render it probable that the mode of formation, above sketched, observable in the Sauropsida and some Mammals, is by

no means the most primitive. In certain Mammals the history of the amnion is very different, and an explanation of the facts appears to be best sought by regarding certain of those modes of formation as more primitive than what we find in the Rabbit or the Fowl. In the Hedgehog (Fig. 1151), for example, there is no up-

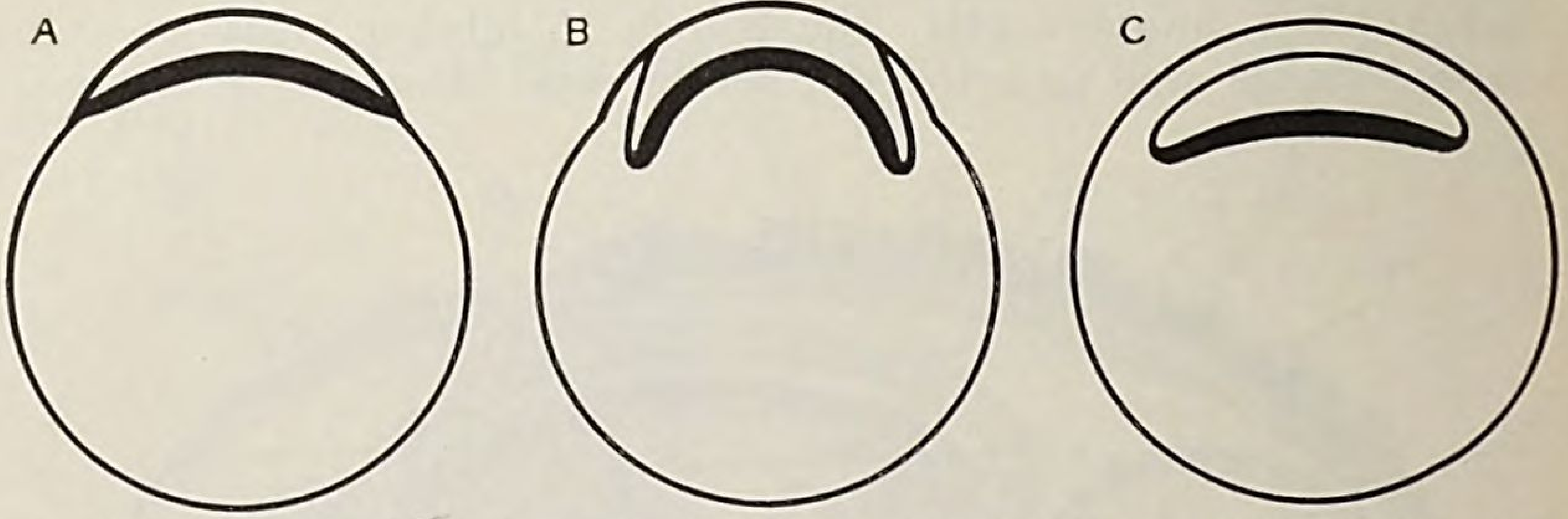


FIG. 1151.—*A*—*C*, diagram illustrating the formation of the **amnion** and **trophoblast** in the **Hedgehog.** Only the ectoderm is represented. *A*, early stage in which a layer of ectoderm destined to form both amnion and the neighbouring portion of the trophoblast has become separated off from the embryonic ectoderm (represented by the thick band) by a distinct space which will become the amniotic cavity ; *B*, later stage in which the trophoblast is becoming separated from the amnion at the sides ; *C*, stage of the complete separation of the trophoblast as a vesicle enclosing the entire blastodermic vesicle as well as the amnion. (After Hubrecht.)

growth and coalescence of folds of the ectoderm or somatopleure ; instead, the upper portion of the ectoderm over the embryonic area becomes split off from the underlying ectoderm destined to become the ectoderm of the embryo (*A*), remaining continuous with it round the edges, but separated by a distinct space

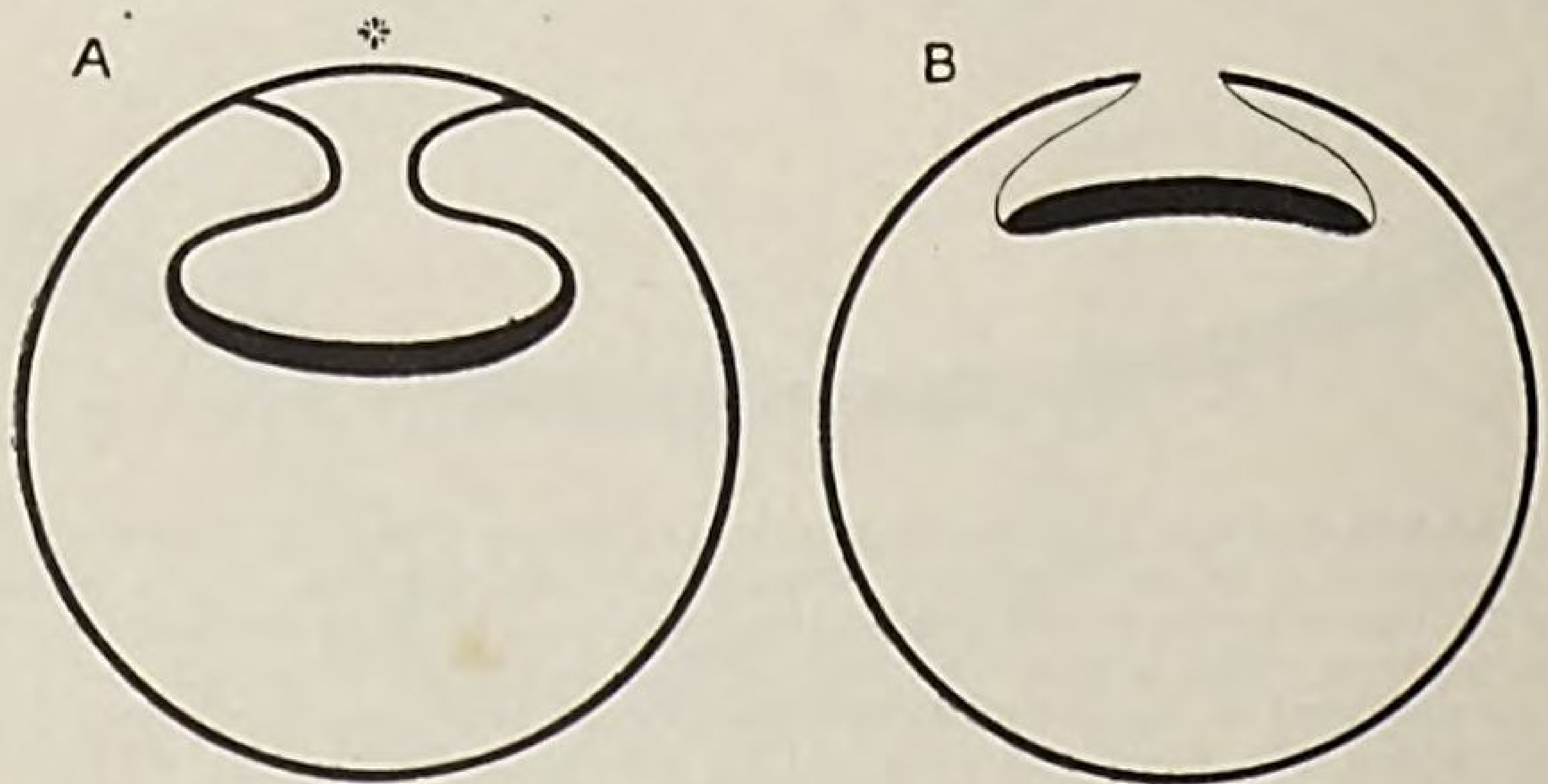


FIG. 1152.—Diagram illustrating the mode of formation of the **amnion** in various Mammals. *A*, commencing formation of the amnion in Mus, Arvicola, etc. The asterisk marks what corresponds to the portion of the trophoblast overlying the embryo in Fig. 1151, *C* ; *B*, mode of formation of the amnion in many Mammals. The portion of the trophoblast indicated by the asterisk in *A* disappears before the amniotic folds make their appearance. (After Hubrecht.)

(destined to give rise to the amniotic cavity) over the body of the embryo itself. This layer of ectoderm then divides (*B*) into two strata—an outer, the *trophoblast* or ectoderm of the serous membrane, and an inner, the ectoderm of the amnion. The former becomes afterwards extended, by the extension of the splitting off of the surface layer of ectoderm, over the entire surface

of the blastodermic vesicle, for which it forms a complete investment (C). In Mus, Arvicola, and others (Fig. 1152, A), the amnion is developed from a series of folds of the ectoderm which arise beneath the trophoblast. In other Mammals (B) the amnion arises in the manner already described, and the portion of the trophoblast immediately overlying the embryonic part of the ectoderm eventually disappears.

The view that the mode of development of the amnion exemplified in the Hedgehog is the most primitive known, is sustained by the consideration that since the function of the amnion with its enclosed fluid is without doubt to protect the delicate embryo from shocks by acting as a sort of water-cushion, it would be entirely useless until the folds had all coalesced, and the view that it arose phylogenetically by the formation of folds, which only after a considerable time coalesced, is rendered improbable.

The allantois has, in all essential respects, the same mode of development as in the Bird, arising as a hollow outgrowth from the hinder part of the alimentary canal; this, growing out into the space between the serous membrane and the amnion, becomes in all the Eutheria applied to the former, and unites with it to form the *chorion*. Sometimes, as in the Rabbit (Fig. 1150), the union between the allantois (TA) and the serous membrane is limited to a comparatively small part of the extent of the latter, but in most instances the allantois spreads over the entire inner surface of the serous membrane, and becomes united with the latter throughout its entire extent. Villi, into which mesoderm with blood-vessels penetrates, grow out from the surface of the chorion and are received into depressions or *crypts* in the mucous membrane of the uterus, which becomes profoundly modified. The villi become branched and enter into intimate union with the uterine mucous membrane, so that a close connection becomes established between the vascular system of the fœtus and that of the parent.

The term *placenta* is applied to the entire structure by means of which this connection is brought about; the parts derived from the embryo are termed the *fœtal placenta*, those developed from the wall of the uterus the *maternal placenta*. In some Mammals the union between the two is not very close, so that at birth the villi of the chorion are simply withdrawn from the crypts of the uterine mucous membrane, no part of the latter being thrown off; such a placenta is said to be *non-deciduate*. In other Mammals the union is closer, and at birth a part of the hypertrophied mucous membrane is thrown off in the form of a *decidua*; such a placenta is termed *deciduate*. In the Mole and the Bandicoot not only is there no decidua thrown off, but the fœtal placenta with the distal portion of the allantois does not pass out after the fœtus,

but remains, and is broken up or absorbed in the uterus. Such a condition has been termed *contra-deciduate*.

In the simplest form of placenta—the *discoidal*—found in the Rabbit and other Rodents (Fig. 1150), the yolk-sac extends over the surface of the serous membrane and becomes fused with it, except in a small area on the dorsal side of the embryo. In this small area the allantois becomes applied to the serous membrane and coalesces with it to form the chorion, from which vascular villi grow out, and are received into the uterine crypts. In most Mammals, however, as already stated, the allantois becomes applied to the serous membrane throughout its entire extent, and the chorion thus completely encloses the embryo. Villi may be developed from all parts of the chorion, except at the poles: when this condition persists in the fully-formed placenta, the term *diffuse* is applied. Sometimes the diffuse condition is temporary, and the completed placenta has villi disposed in a broad band or zone (*zonary* placenta). Sometimes the villi are grouped together in patches or cotyledons (*cotyledonary* placenta). In Man and the Apes the villi become restricted to a disc-shaped area of the chorion situated on the ventral side of the embryo (*meta-discoidal* placenta).

The stalk of the yolk-sac, with the corresponding narrowed part of the allantois and the vessels which it contains, forms the *umbilical cord* by which the fœtus is connected at the umbilicus with the yolk-sac and placenta. This is enclosed in a sheath formed by the ventral portion of the amnion. The part of the allantois which remains within the cavity of the body develops into the urinary bladder, together with a cord—the *urachus*—connecting the bladder with the umbilicus.



FIG. 1153.—Mammary fœtus of **Kangaroo** attached to the teat. (Natural size.)

The developmental history of the Marsupials differs from that of the Eutheria in the transitory character or entire absence of a placental connection between the fœtus and the uterine mucous membrane. The intra-uterine development of the fœtus is abbreviated, and birth takes place when the young animal is still relatively very small and has many of the parts incompletely formed. In this helpless condition the young Marsupial is placed by the mother in the marsupium, where it remains for a time as a *mammary fœtus* (Fig. 1153), hanging passively to the teat, to which the mouth becomes firmly adherent. The milk is expressed from the mammary gland by the contraction of a muscle, the *cremaster*, and passes down the gullet of the fœtus,

which is enabled to breathe unobstructedly through the nostrils by the establishment of a continuous passage from the nasal cavities to the larynx, as already described (p. 544).

In all the Marsupials, so far as known, the embryo is covered over, except in a limited area, by the compressed and expanded

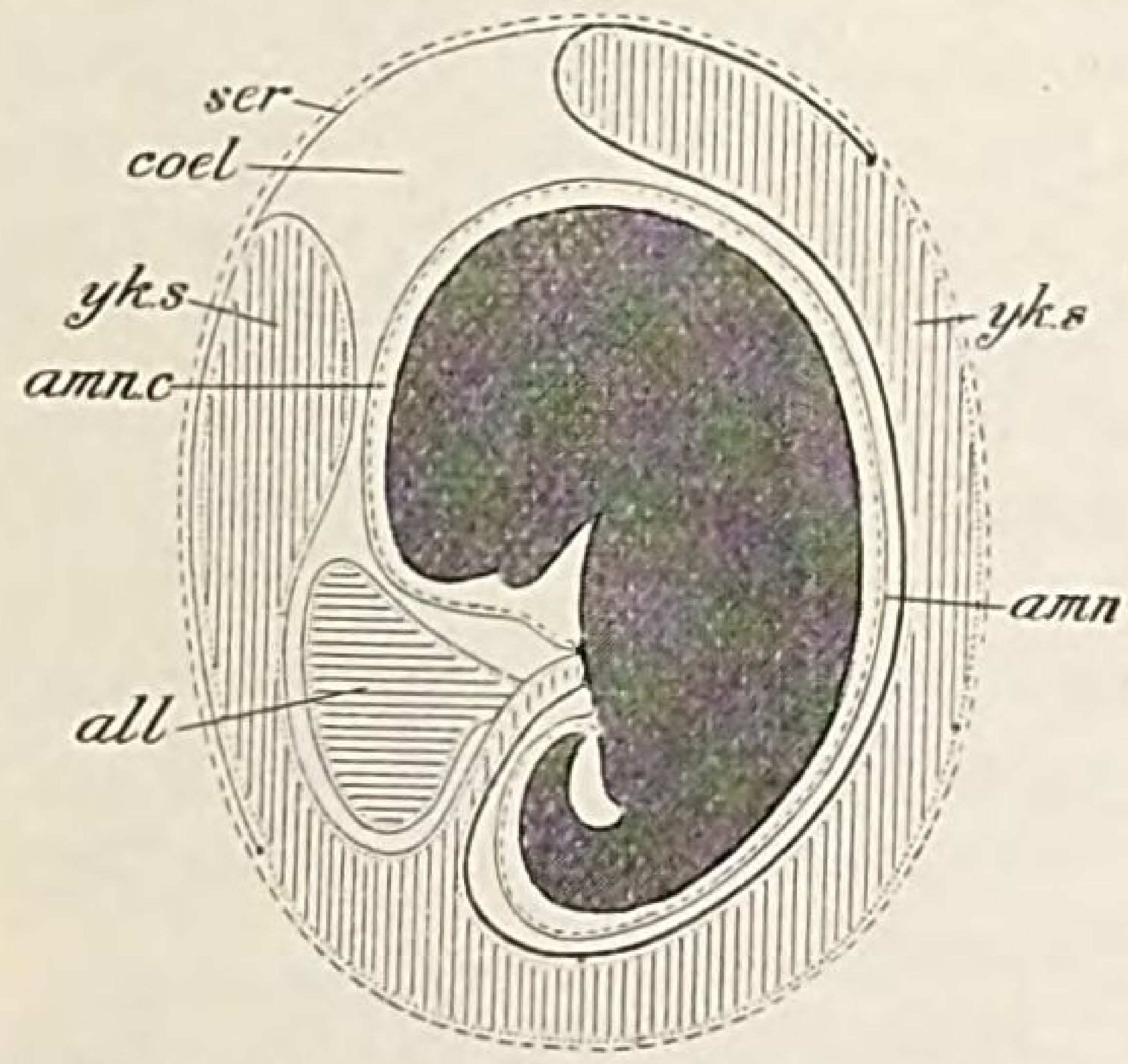


FIG. 1154.—Diagram of the embryo and fœtal membranes of **Hypsiprymnus rufescens.** *all.* allantoic cavity; *amn.* amnion; *amn. c.* cavity of amnion; *cœl.* extra-embryonic cœlome; *ser.* serous membrane; *yk.s.* yolk-sac. (After Semon.)

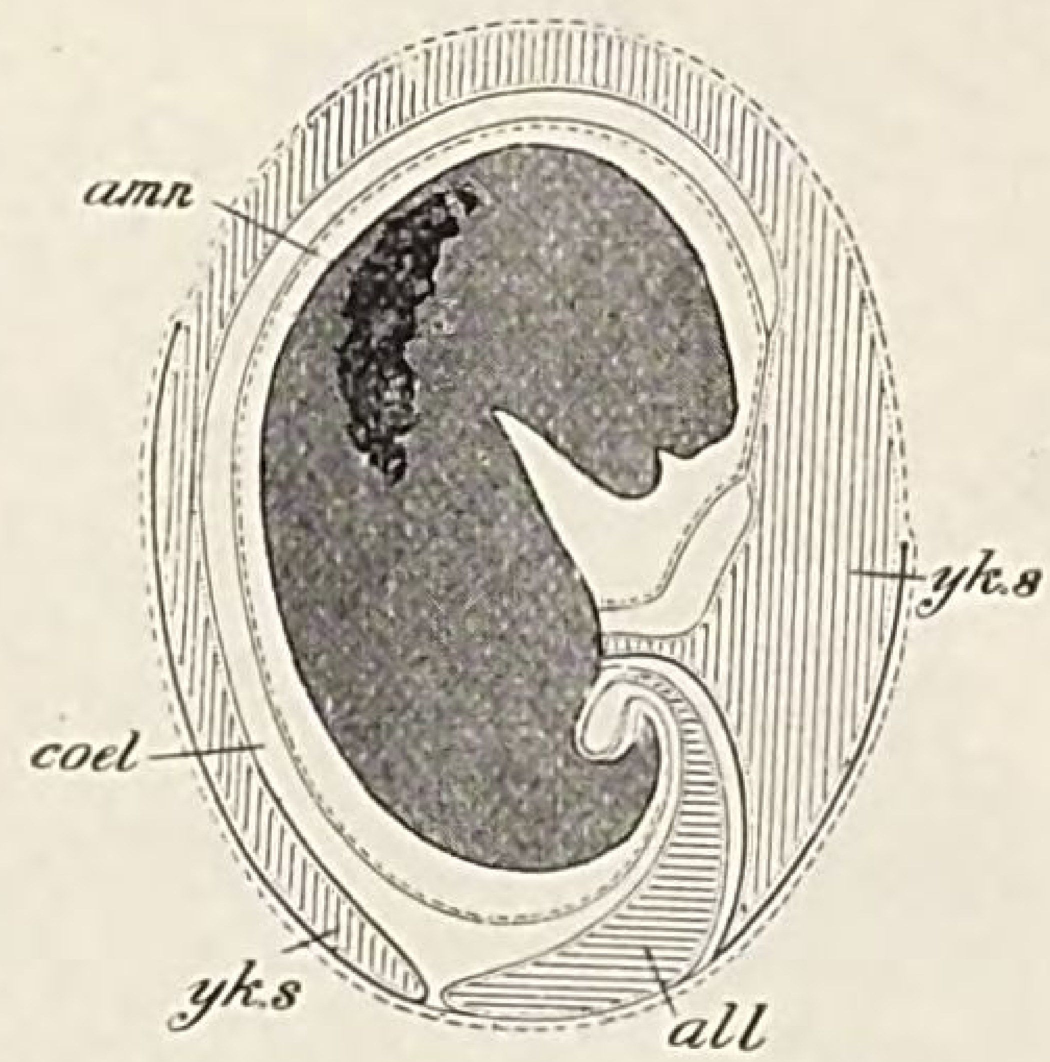


FIG. 1155.—Diagram of the embryo and fœtal membranes of **Phascolarctos cinereus.** Letters as in Fig. 1154. (After Semon.)

yolk-sac. In the majority (Fig. 1154) the allantois (*all.*) is small and is completely enclosed with the embryo in the yolk-sac. In the Koala, however (Fig. 1155), it stands out and becomes closely applied to the serous membrane over the small area not covered by the yolk-sac; but no vascular villi are developed. Only in the Bandicoots (Fig. 1156), so far as known, is the outgrowth of the allantois to the serous membrane followed by the establishment of a true placental connection by the development of vascular villi received into uterine crypts.

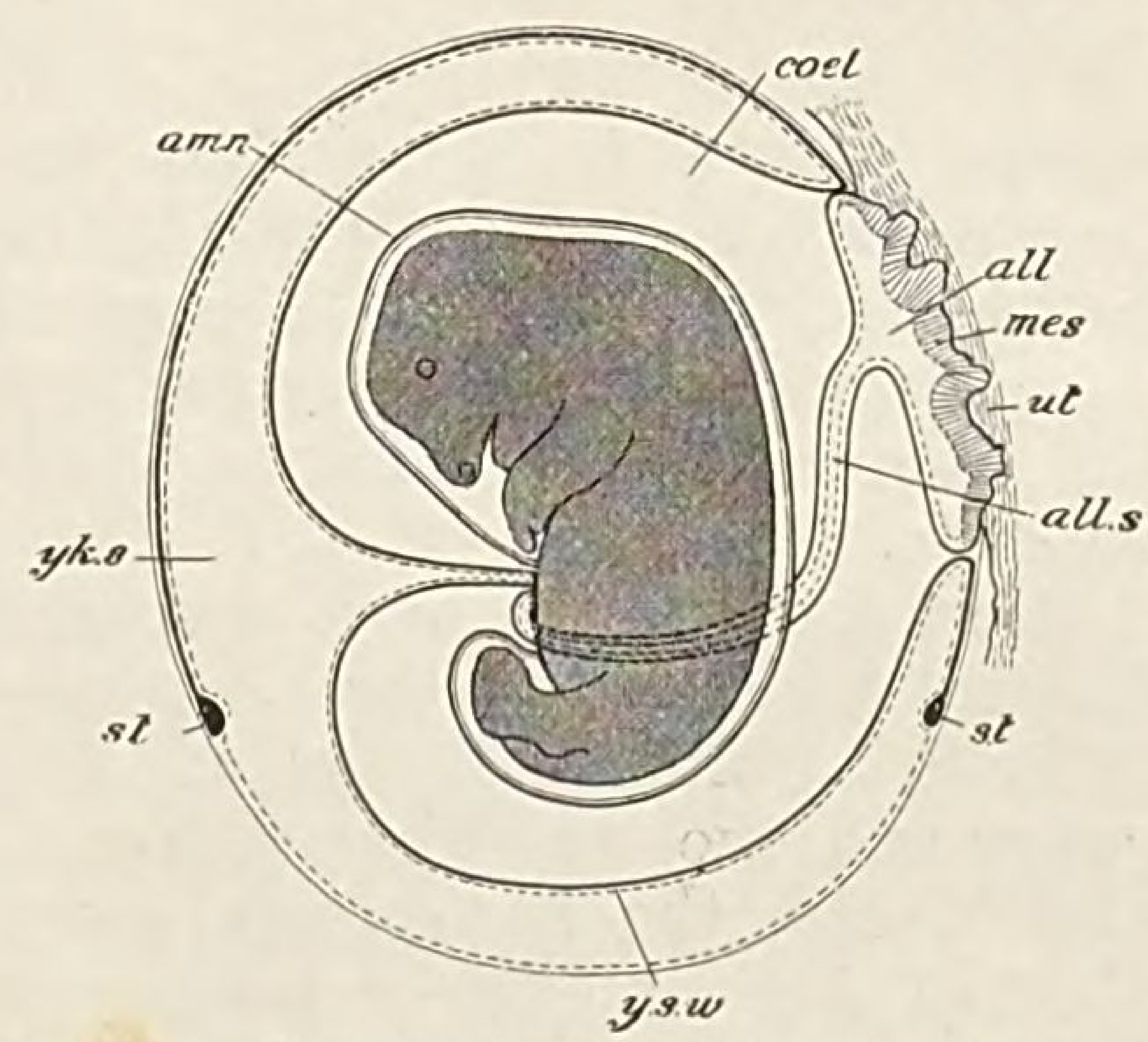


FIG. 1156.—Diagram of the embryo and placenta of **Perameles obesula.** Letters as in Fig. 1154. In addition, *all. s.* allantoic stalk; *mes.* mesenchyme of outer surface of allantois fused with mesenchyme of serous membrane; *s. t.* sinus terminalis; *ut.* uterine wall. (After J. P. Hill.)

The Prototheria, unlike all the rest of the Mammalia, are oviparous. In Echidna only a single egg, as a general rule, is laid in a season. This is placed in a temporary marsupium, formed as already described (p. 464) in the mammary region of the ventral surface. The young animal soon emerges from the egg, and

remains enclosed in the marsupium till it reaches an advanced stage of development. Ornithorhynchus develops no marsupium, and the two eggs which it produces are deposited in its burrow. In Echidna the egg-shell is composed of keratin; in Ornithorhynchus, it contains carbonate of lime. The ova of the Prototheria are very much larger than those of other Mammals (Fig. 1157), their large dimensions being due to the presence of a large proportion of food yolk. The segmentation, unlike that of all the Theria, with the exception of the Koala, is meroblastic.

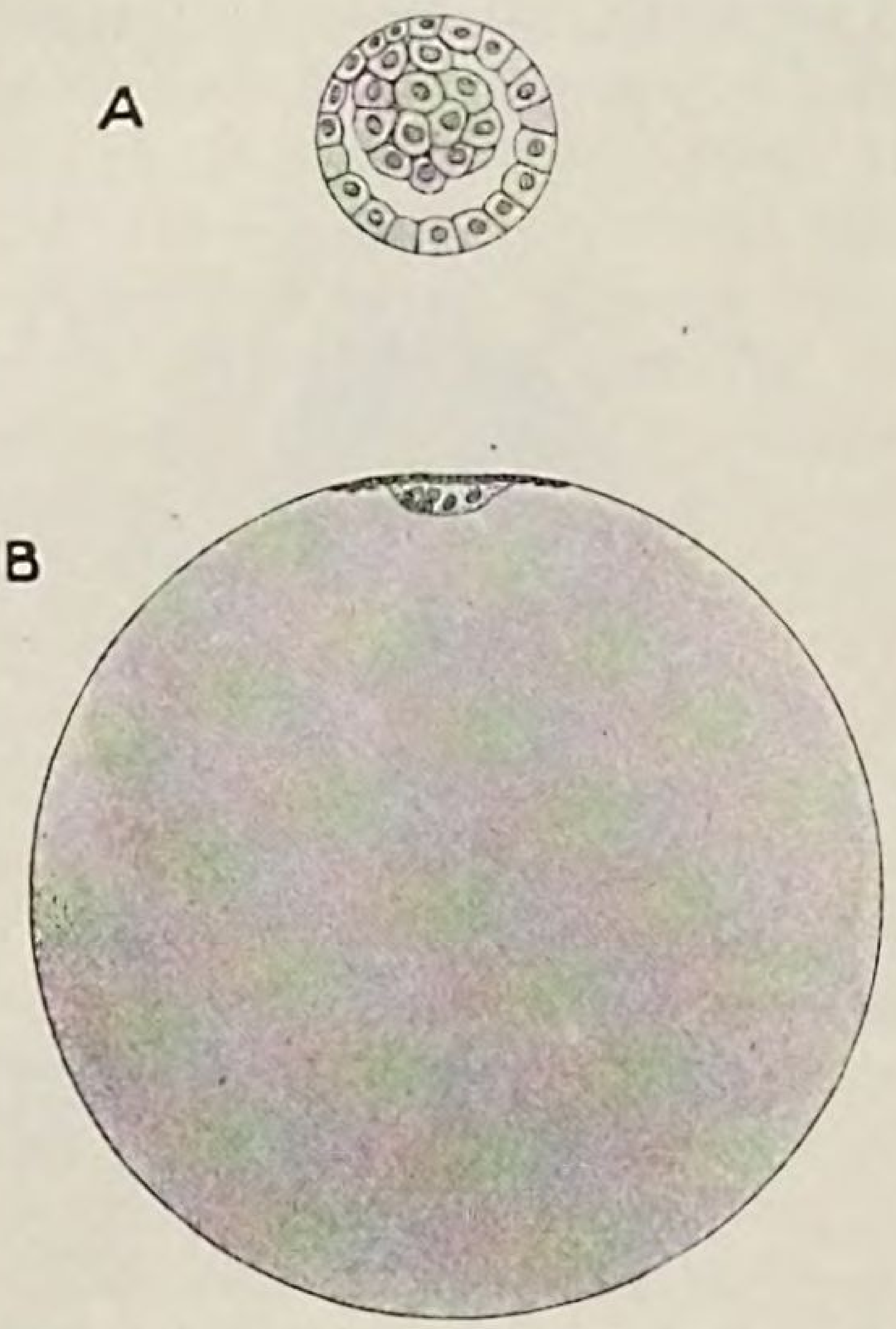


FIG. 1157.—*A*, blastula stage of one of the **Theria.** *B*, transition stage between the morula and blastula in a **Monotreme.** Both represented in diagrammatic section. (After Semon.)

Distribution.—The Monotremes are entirely confined to Australia, Tasmania, and New Guinea. The Marsupials are most abundantly represented in the Australian region, the greater number of the Australian families and genera being restricted to the Australian continent, and to Tasmania, though several genera extend to New Guinea and some of the neighbouring islands. The family Didelphyidæ, or Opossums, inhabits South America and extends into the southern part of North America; and a single genus *Cænolestes* of a family related to the Australian Diprotodonts has been recently found in South America.

The Edentates are most numerously represented in South and Central America, the true Ant-eaters, the Sloths, and the Armadillos being all inhabitants of that region. But the Scaly Ant-eaters and the Ard-varks (Cape Ant-eaters) are denizens of the Old World; the former inhabiting Southern Africa and South-Eastern Asia, the latter being confined to Africa. The Cetacea are cosmopolitan in their distribution: the great majority are marine, but some ascend rivers, and a few are exclusively fluviatile, inhabiting the rivers of South America and South-Eastern Asia.

The distribution of the Sirenia is somewhat restricted. The recently extinct Rhytina inhabited Behring's Straits. The Manatee is confined to the Atlantic coasts of South America and of Africa, living chiefly in the larger rivers. The Dugong occurs on the east coast of Africa, in the Red Sea, the Indo-Malayan

islands, and the northern coast of Australia. The Ungulata occur in all the great regions, with the exception of the New Zealand, Polynesian, and Australian. Oxen are, with the exception of the American Bison, natives of the Palæarctic, Ethiopian, and Oriental regions. Wild Sheep, with the exception of one African and one North American species, are confined to the Nearctic and Oriental regions. Goats are also mainly Nearctic and Oriental. Antelopes are confined to the Old World, and are by far more numerous in the Ethiopian than in other regions. The Prongbucks are Nearctic; the Giraffes exclusively Ethiopian. Deer are widely distributed in the Nearctic, Neotropical, Palæarctic, and Oriental regions, but are absent from the Ethiopian. The Camels are natives of the Old World; the Llamas of the Neotropical region. Wild species of Pigs are widely distributed in the Old World and are absent in the New; while the Peccaries are confined to the Nearctic and Neotropical regions. Hippopotami are confined to Africa. The Horses, including the Zebras and Asses, are restricted at the present day, as regards their natural distribution, to the Old World, though they abounded also in America in the Pleistocene period. Rhinoceroses are Oriental and Ethiopian. Tapirs have a singular distribution, one species occurring in the Malay Archipelago, and the rest in the Neotropical region. Hyraxes are confined to Africa, Arabia, and Syria. Of the Elephants, one species is confined to the Oriental, the other to the Ethiopian regions, but fossil-remains prove that in Pleistocene times the range of the Elephants, and their gigantic extinct allies, the Mammoths, was very much wider, and extended over Northern Africa and the entire Palæarctic region. Only one fossil species has been found in America.

Carnivora, if we leave out of account the Australian Dingo or Native Dog, are absent in the Australian, Polynesian, and New Zealand regions, but range over all the other geographical provinces. The Cats and the Dogs are found in all parts of this extensive area; the Hyænas are restricted to the Western part of the Oriental region and the warmer parts of the Holarctic and the Ethiopian. The Civets are most abundant in Africa, Madagascar, and South-Eastern Asia, but occur also in the Southern parts of Europe; and many of the smaller groups have a yet more restricted range. Bears have a wide distribution, but are absent from the whole of the Ethiopian region.

The majority of the Pinnipedia are found in the Arctic and Antarctic regions, and in the temperate zones of both hemispheres, few ranging into the tropics. The Walruses are almost exclusively Northern, while the Eared Seals and Earless Seals are almost equally abundant in the Northern and Southern hemispheres.

The Rodents have a wider range than any other of the orders of land Mammals, and occur in all parts of the globe, though they are

poorly represented in Australia and Madagascar. The Rodents reach their greatest development, as regards the number of families, in South America, in which region occur also the majority of the largest members of the order.

Insectivora are absent in the Australian, Polynesian, and New Zealand regions, and in South America; but occur in all the other provinces. The Chiroptera are world-wide in distribution, occurring in greatest abundance in tropical and warm temperate zones. The Flying Foxes (Pteropidæ) are absent from the Nearctic and Neotropical regions, and the Vampire Bats occur exclusively in the latter.

The distribution of the Lemurs is remarkable; they occur only in Madagascar, a limited part of South Africa, Southern India and Ceylon, some of the islands of the Malay Archipelago, and the Philippines. The headquarters of the group is the island of Madagascar, of which they constitute one-half of the entire Mammalian fauna.

Of the other groups of Primates, the Marmosets (Hapalidæ) and the Cebidæ are exclusively American; the Cercopithecidæ Palæarctic, Oriental and Ethiopian, with a single species in Madagascar. Of the Simiidæ the Gibbons occur only in South-Eastern Asia and the Malay Peninsula; the Orangs only in Borneo and Sumatra; the Gorilla and Chimpanzee in certain parts of Western Equatorial Africa.

The earliest fossil-remains of Mammals have been found in strata of Upper Triassic and of Jurassic age in Europe and America. These remains consist almost exclusively of jaws and teeth, and,

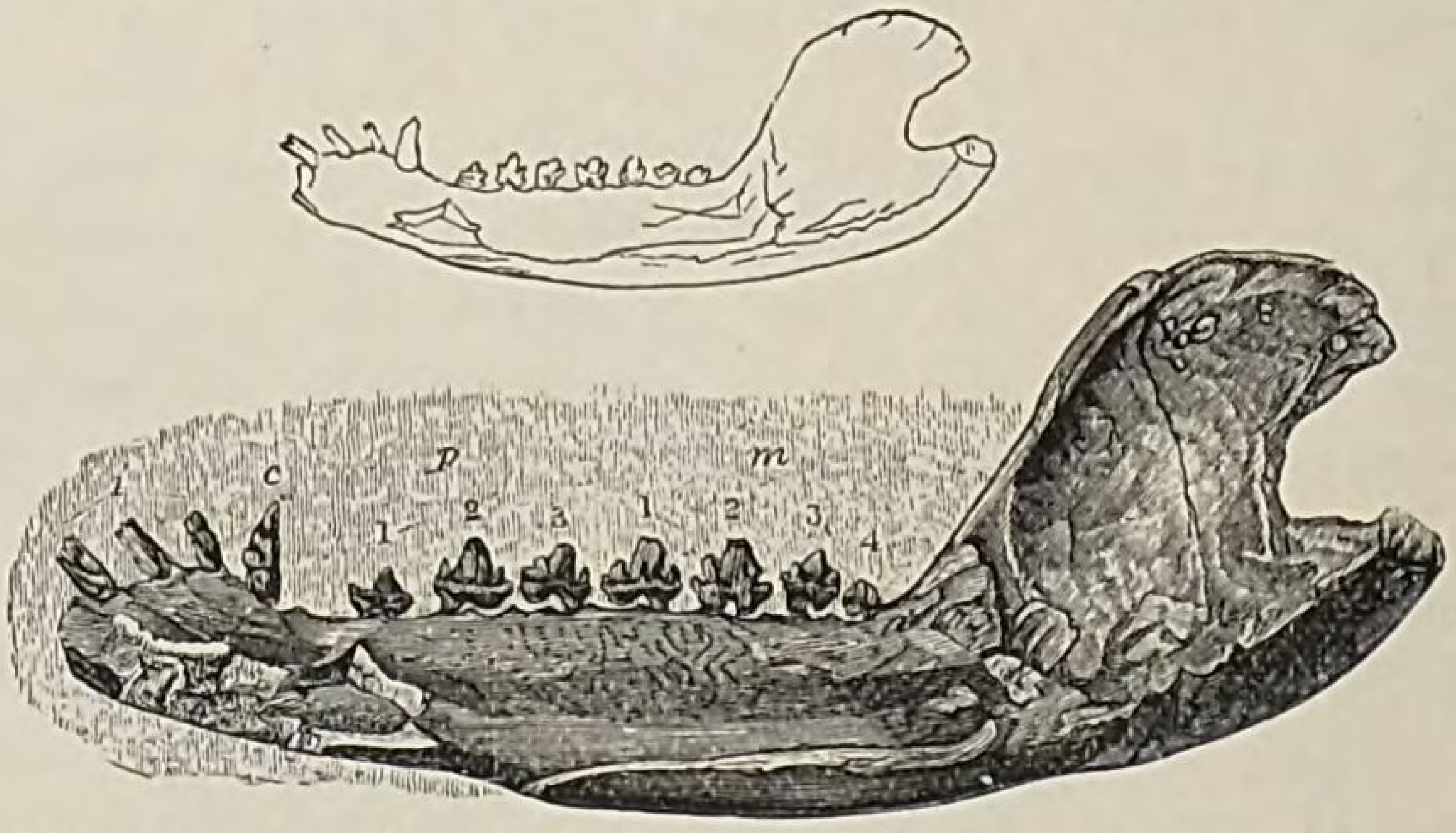


FIG. 1158.—**Phascolotherium bucklandi.** Inner view of right ramus of mandible. (After Owen.)

as the latter differ widely from those of existing Mammals, there is frequently great difficulty, in the abs nce of remains of the other hard parts, in determining the affin ties of these Mesozoic forms. Some of the Triassic and Jurassic Mammalian molar teeth are constructed on the most primitive form of the triconodont type, which has already been referred to (p. 529) as being the primitive

form in the class, having three cones or cusps in a longitudinal row. In *Dromatherium* and its allies each molar has a single main cusp with two smaller accessory cusps. There is no decisive evidence as to the affinities of these primitive triconodont Mammals, but they may be provisionally set down as allied to the Prototheria.

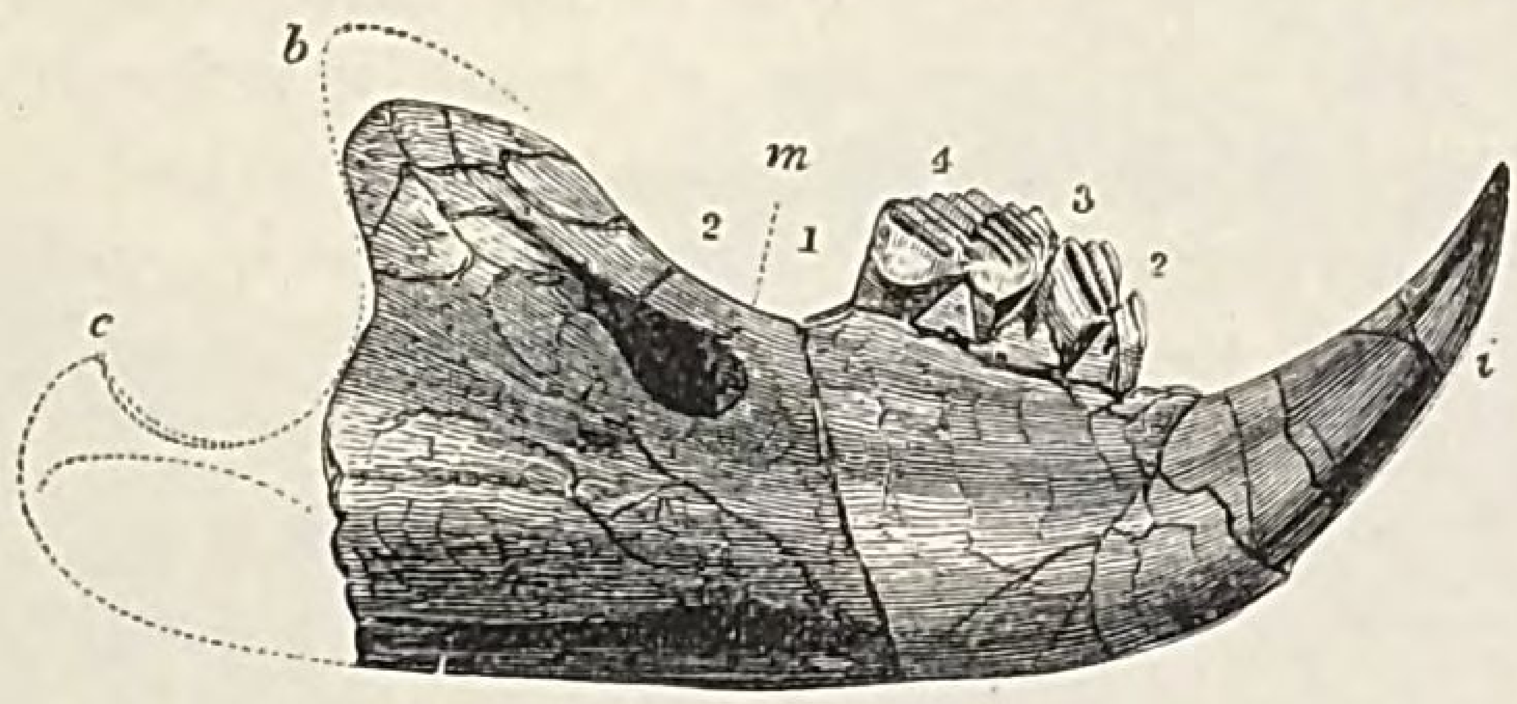


FIG. 1159.—**Plagiaulax becklesi.** Mandible with teeth. (After Owen.)

Of the remainder of the Mesozoic Mammals some were probably Prototheria, others Metatheria, while others again may have been Insectivores. Most of them fall into two main groups. The type of dentition presented by the members of one of these groups (Fig. 1158) is more nearly allied to that of the Polyprotodont Marsupials (p. 530) than to any other. In the other group (Multituberculata) (Fig. 1159) there is a superficial resemblance to the Diprotodont Marsupials; there is a single chisel-shaped incisor on each side of the lower jaw, and one large, and sometimes one or two smaller, on each side of the upper. A wide diastema separates these from the pre-molars. The molars present longitudinal rows of tubercles. In some cases the pre-molars have a pattern similar to that exhibited by the molars, but in others they have a cutting edge which may be serrated or obliquely grooved. An essential difference between this dentition, and that of the existing Diprotodont Marsupials, in addition to the peculiar structure of the molars, is that in the Multituberculata, when the upper incisors are fewer than three, the large tooth which bites against the large incisor of the lower jaw is the second and not the first. Moreover, the fact that the vestigial molar teeth of Ornithorhynchus come nearer in pattern to those of the Multituberculata than to those of any other known group seems to indicate that the affinities of the latter are rather with the Prototheria than with the Metatheria.

Fossil remains of Mammals belonging to the Cretaceous age are known only from certain limited beds in North America. But in deposits of the succeeding Tertiary period there have been found the remains of an extensive and varied Mammalian fauna. The earlier Tertiary Mammals in many cases present features which enable us without hesitation to refer them to one or other of the existing orders; but when this is the case there is nearly always to

be recognised an absence, or a less advanced development, of some of the more salient characteristics; in other words, the earlier Tertiary Mammals, when referable to existing orders, are less highly specialised than the living representatives of these orders. No less significant is the fact that these early Tertiary representatives of existing orders had the cavity of the brain-case nearly always much smaller in proportion to the other dimensions than in living forms. But many are not so readily referable to existing orders, sometimes owing to their possessing marked special features of their own, sometimes owing to their combining characteristic features of two or more living orders. Through the series of Tertiary and Post-tertiary formations it is possible to trace a gradual development from the early generalised, to the existing specialised, genera, and in some instances by such gradual transitions that the actual course of the evolution can be followed stage after stage. There is only space here for a very brief review of this extensive and remarkable Tertiary and Post-tertiary Mammalian fauna.

No remains of Prototheria are known from the Tertiary, and it is only when we come to Post-tertiary (Pleistocene) that we meet with fossil representatives of the group. These, which have been found only in Australia, differ little from the existing Echidna.

Of the Marsupials the Opossums (Didelphyidæ) of America are represented not only in Tertiary and Pleistocene deposits in that continent, but in beds of the former age in Europe. In addition, in certain European deposits of Eocene age, there occur teeth and jaws which may be Marsupial in character, but the affinities of which are uncertain; and in Tertiary deposits of South America

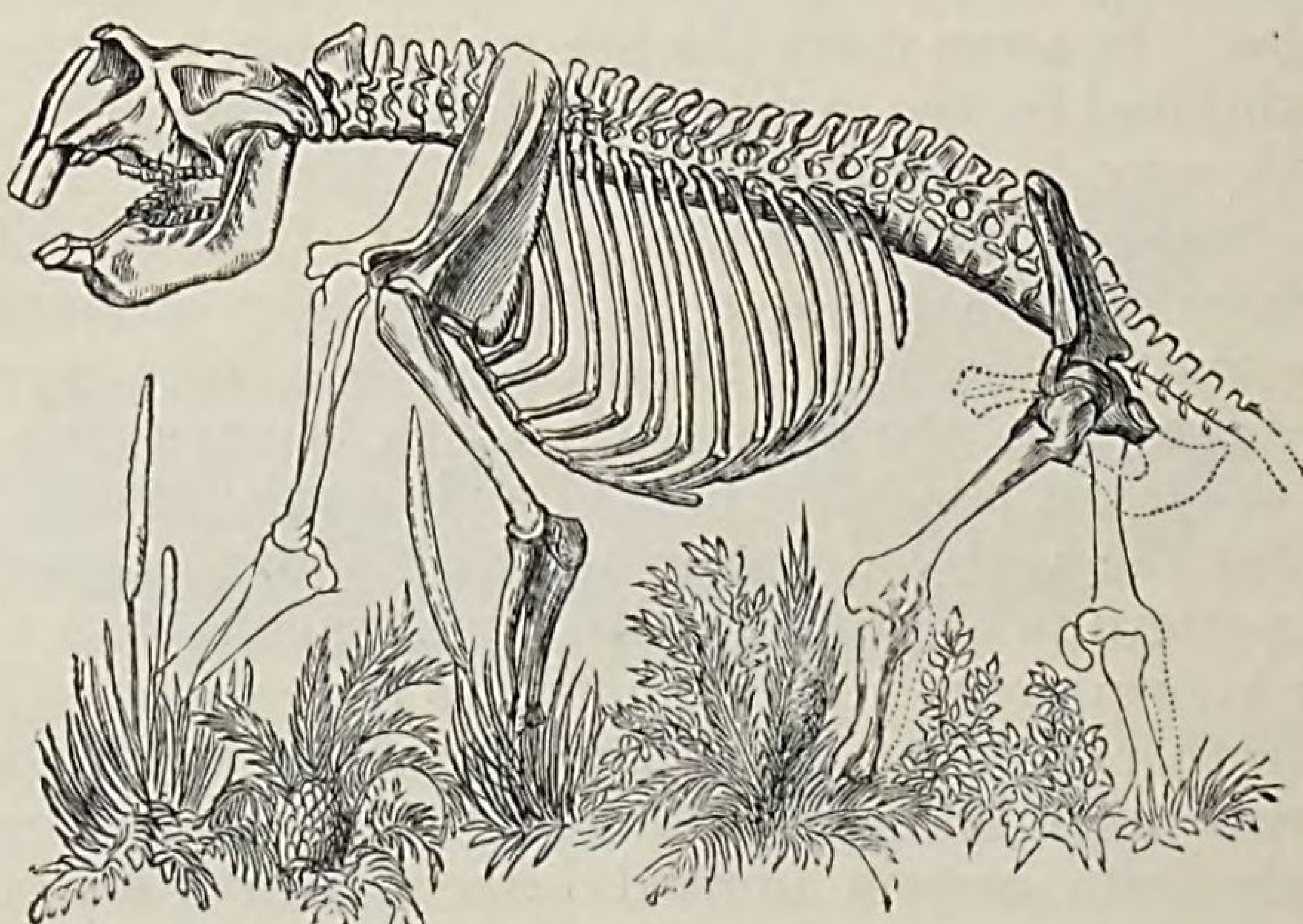


FIG. 1160.—**Diprotodon australis.** (After Owen.)

have been found numerous remains of Diprotodonts. The remainder of the fossil Marsupials hitherto discovered are of Pleistocene age, and have all been found in Australia. The Australian

Pleistocene Marsupials are for the most part referable to existing families and even genera, representing both the Diprotodont and the Polyprotodont sections; but some differ widely from existing forms. One of these, *Diprotodon* (Fig. 1160), was the largest

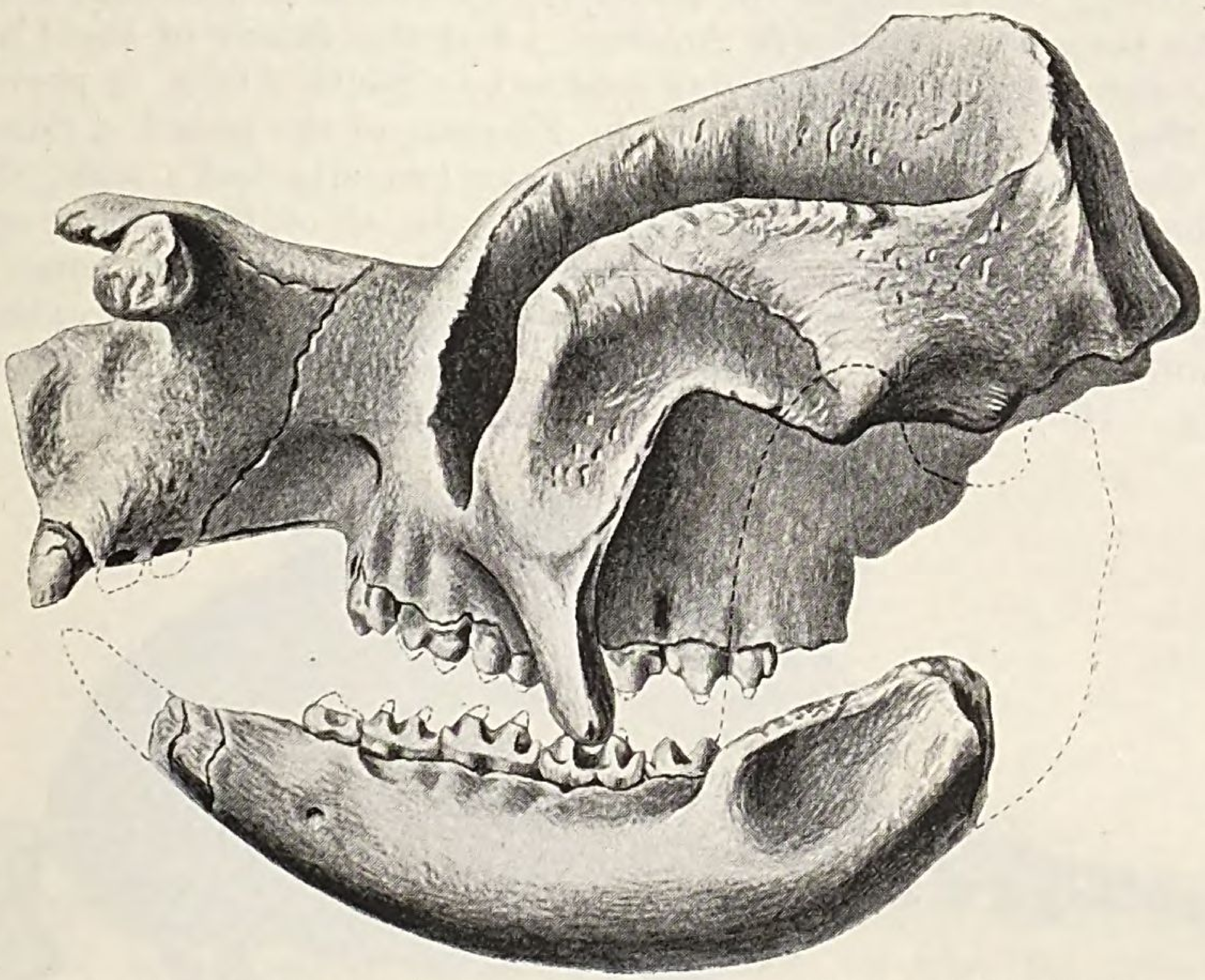


FIG. 1161.—**Nototherium mitchelli.** Side view of skull. (After Owen.)

known Marsupial, having reached the dimensions of a Rhinoceros; it occupies a position intermediate between the Phalangers and the Kangaroos. *Nototherium* (Fig. 1161), also of large

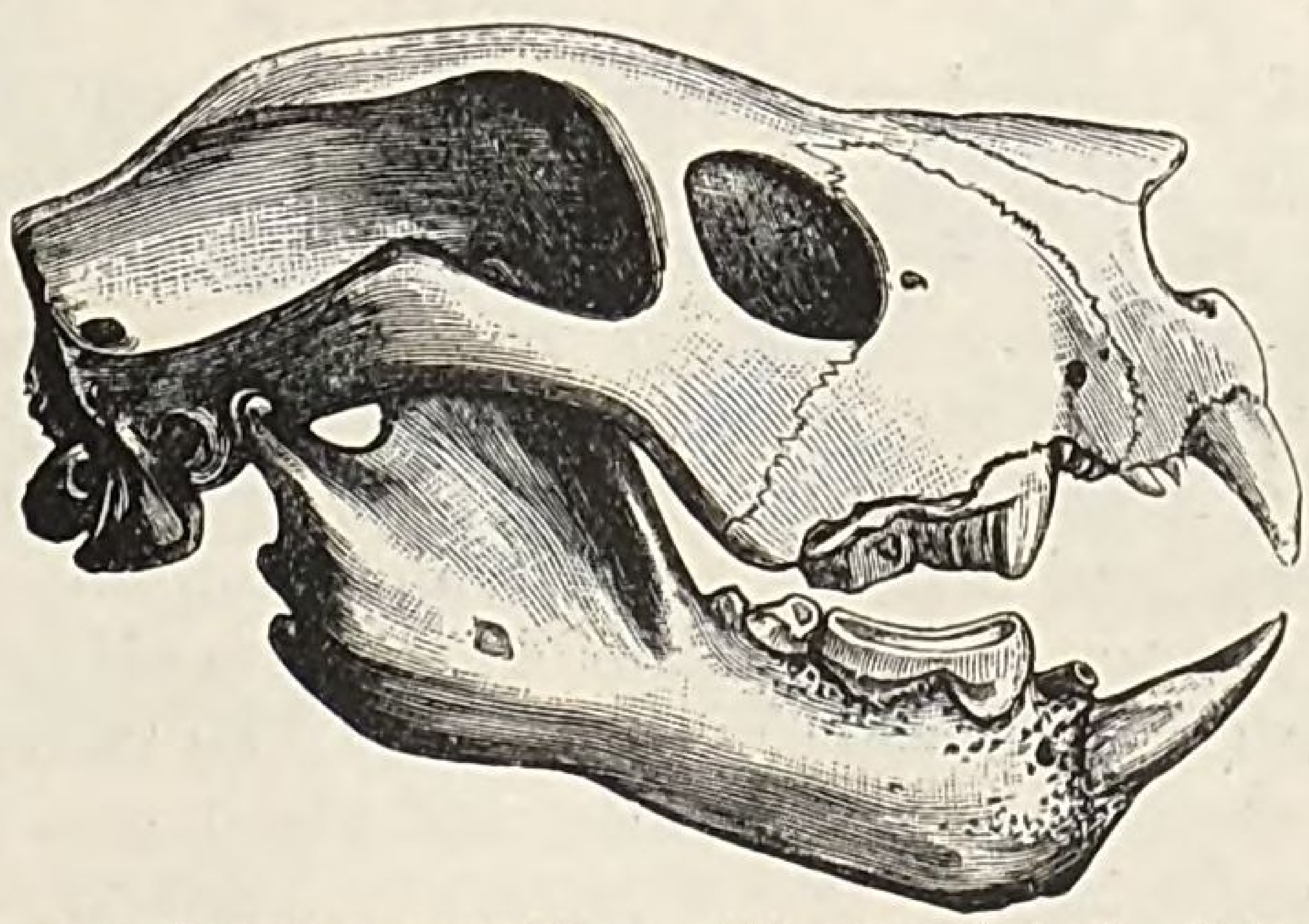


FIG. 1162.—**Thylacoleo carnifex.** Side view of skull. (After Flower.)

size, seems to connect together the Diprotodon, the Wombats, and the Phalangers. *Thylacoleo* (Fig. 1162) is an extinct genus referable to the Phalanger family, and characterised by an

extremely modified dentition, the only functional teeth being a single pair of large incisors in the middle in both upper and lower jaws, with a single elongated trenchant pre-molar on each side both above and below.

Among the Edentata the majority of fossil, as of existing, forms have been found in South America. But the family of the Cape Ant-eaters, at the present day confined to South Africa, is proved, by the discovery of remains in the Pliocene of the island of Samos in the Eastern Mediterranean, to have formerly had a wider distribution. The American fossil Edentata, all of Pleistocene age, comprise, in addition to extinct genera of Armadillos, some of gigantic size, and one of Sloths, representatives of two extinct families, the *Glyptodontidæ* and the *Megatheriidæ*. The former (Fig. 1163) are large Edentates resembling the Armadillos in

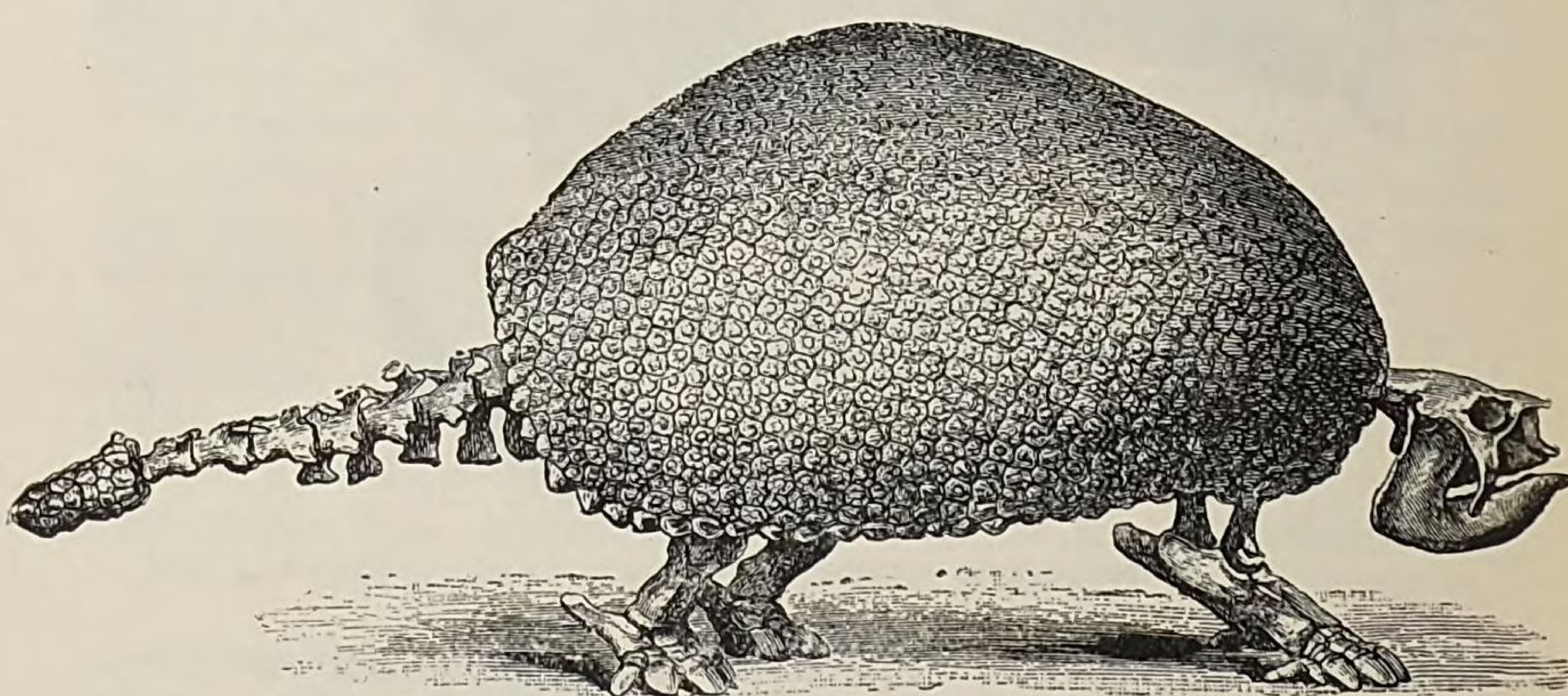


FIG. 1163.—**Glyptodon clavipes.** (After Owen.)

the presence of a bony dermal carapace and a bony investment for the tail; but in the Glyptodontidæ the carapace has no movable rings, so that the animal could not roll itself up, and there is usually a ventral bony shield or plastron, never present in the Armadillos. Glyptodonts occur in North as well as in South America. The Megatheriidæ (Fig. 1164) are Edentates, mostly of enormous size and massive build, which combine certain of the features now characteristic of the Ant-eaters (Myrmecophagidæ) and the Sloths (Bradypodidæ) respectively, the spinal column and limbs allying them with the former, and the crania and the teeth with the latter.

The Cetacea are represented in the Tertiary (Eocene and Miocene) of Europe, Egypt, and North America, by an extinct sub-order—the *Archæoceti* or Zeuglodonts, comprising only one known genus—*Zeuglodon*. Zeuglodon differs from existing Cetacea,

mainly in the possession of rooted heterodont teeth, and in the position of the narial aperture, which is situated comparatively far forwards; the limbs are not known. The remains of both Whale-

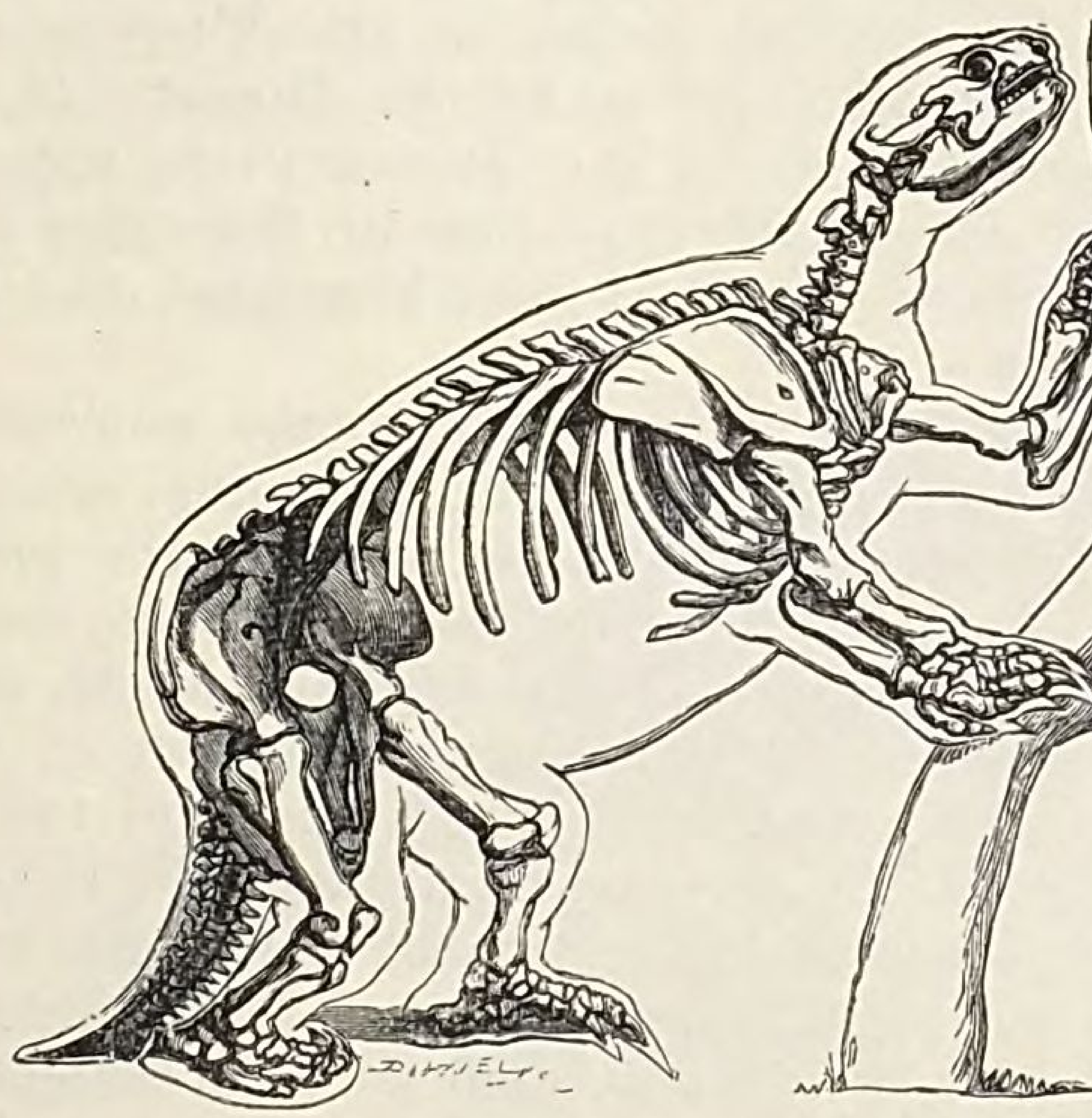


FIG. 1164.—**Mylodon robustus.** (Restoration, after Owen.)

bone Whales and Toothed Whales occur abundantly in Pliocene deposits, some belonging to extinct, others to existing, genera. Toothed Whales occur also in Miocene formations, and there, as well as in the Pliocene and Pleistocene of Europe, North America, New

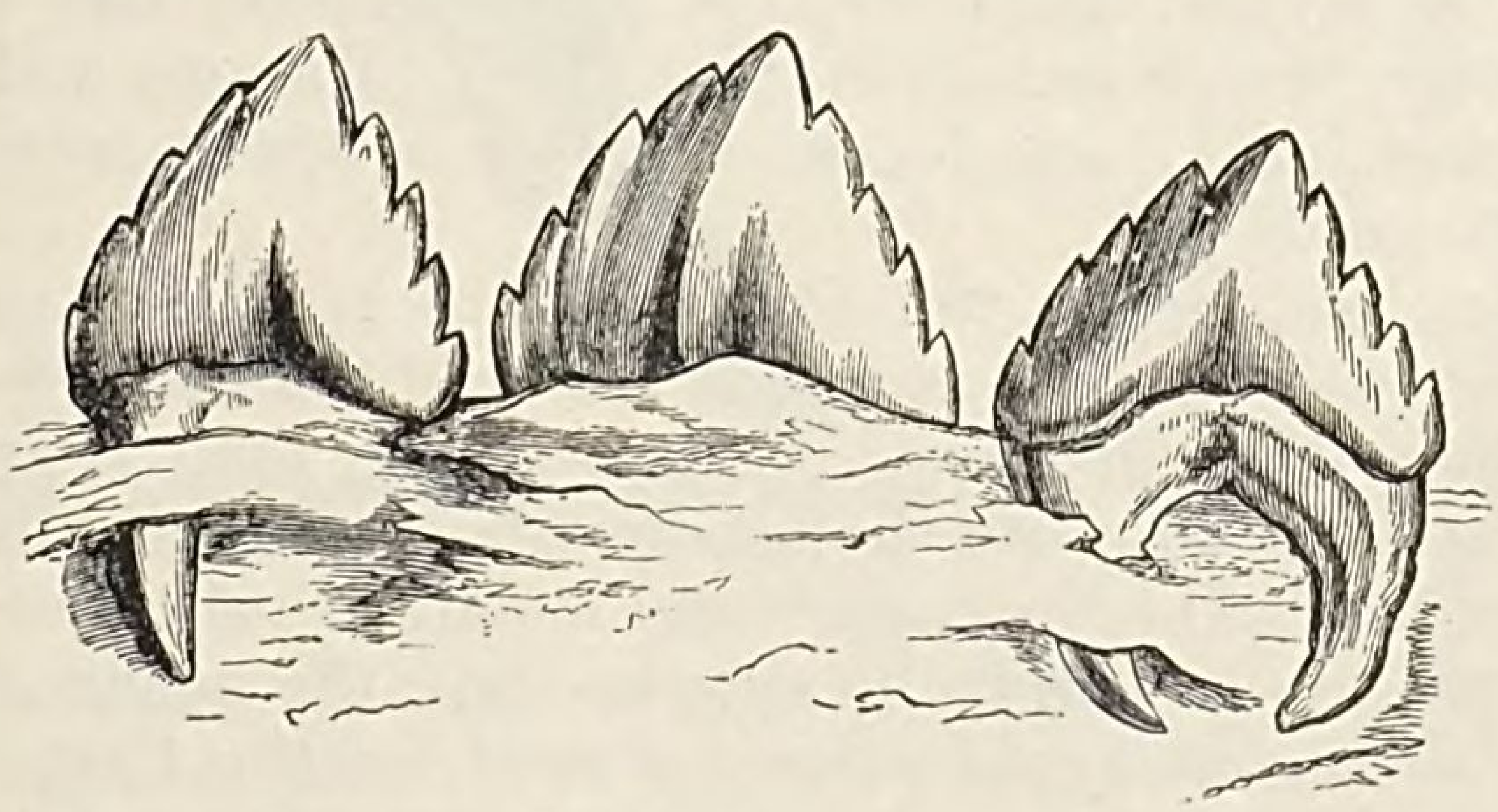


FIG. 1165.—**Squalodon.** Three of the lower true molars. (After Flower.)

Zealand, and Australia, are represented by an extinct family, the *Squalodontidæ* (Fig. 1165), with heterodont dentition.

The order Sirenia is first met with in the Eocene, and was represented in that and succeeding periods by several genera which have become extinct, composing a family—the *Halitheriidæ*—of

which Halitherium is the best known member. These were characterised by the possession of upper incisors, of enamelled pre-molars and molars, of a milk-dentition, and of small vestiges of femora. The family of the Dugongs is represented by a form nearly allied to the existing genus in the Pliocene of France, and probably by another genus in the Tertiary of California. The family of the Manatees is not known to be represented by any fossil forms. Of doubtful position in the order are certain genera that have been described from European and Australian Tertiary formations.

The Tertiary Ungulata comprise an immense number of forms, including a considerable number of extinct families, into an account of which it would be going beyond the scope of the present work to enter. In the Artiodactyle series there is to be traced a progressive union and coalescence of the third and fourth metacarpals to form the cannon-bone, a progressive reduction of the lateral digits, and a progressive development of horns or of tusks—absent or rudimentary in the earlier representatives of the sub-order. In the Perissodactyle series the reduction of the lateral toes reaches its maximum in the existing genus Equus. The history of this reduction, together with the development of other characteristic features, can be traced from pentadactyle forms with simple molars through a long series of gradations to the monodactyle Horses with their complexly folded molars. Similar genealogies, though not always so complete, can be traced for the Tapirs and Rhinoceroses, and for the Deer, Camels, and Pigs.

The order Proboscidea was represented in Tertiary and Pleistocene times, not only by forms allied to those now living, though sometimes, as in the Mammoths, of much greater size, but by an extinct family, the *Dinotheridæ* (Fig. 1166) (Miocene and Pliocene of Europe and India), which possess a pair of downwardly-directed tusks in the lower jaw.

A separate sub-order, the *Condylarthra*, has been established for a number of Eocene Ungulates, which differ somewhat widely from all the other members of that group, and approach the Carnivora in some respects, though having certain resemblances to the Hyracoidea. The pre-molars and molars are short and usually bunodont, the pre-molars being simpler than the molars, the latter sometimes tritubercular, like those of many of the Carnivora; the incisors and canines also sometimes resemble those of the Carnivora. The humerus differs from that of the other Ungulata, and resembles that of the Carnivora in the presence of a foramen over the inner condyle. As in the Hyracoidea the scaphoid articulates with the trapezoid and not with the magnum, and the femur has a third brochanter. The limbs are usually pentadactyle, with pointed ungual phalanges. The astragalus has, as in the Carnivora, a uniformly rounded distal articular surface.

The fibula does not articulate with either the astragalus or the calcaneum.

Another extinct primitive sub-order of the Ungulata is the *Amblypoda*, the members of which have been found, like the Condylarthra, in the Eocene of North America and of Europe. These resemble the Condylarthra and Hyracoidea in the relation of the scaphoid to the trapezoid; both magnum and unciform articulate with the lunar. The fibula articulates with the calcaneum; the cuboid articulates with both the astragalus and

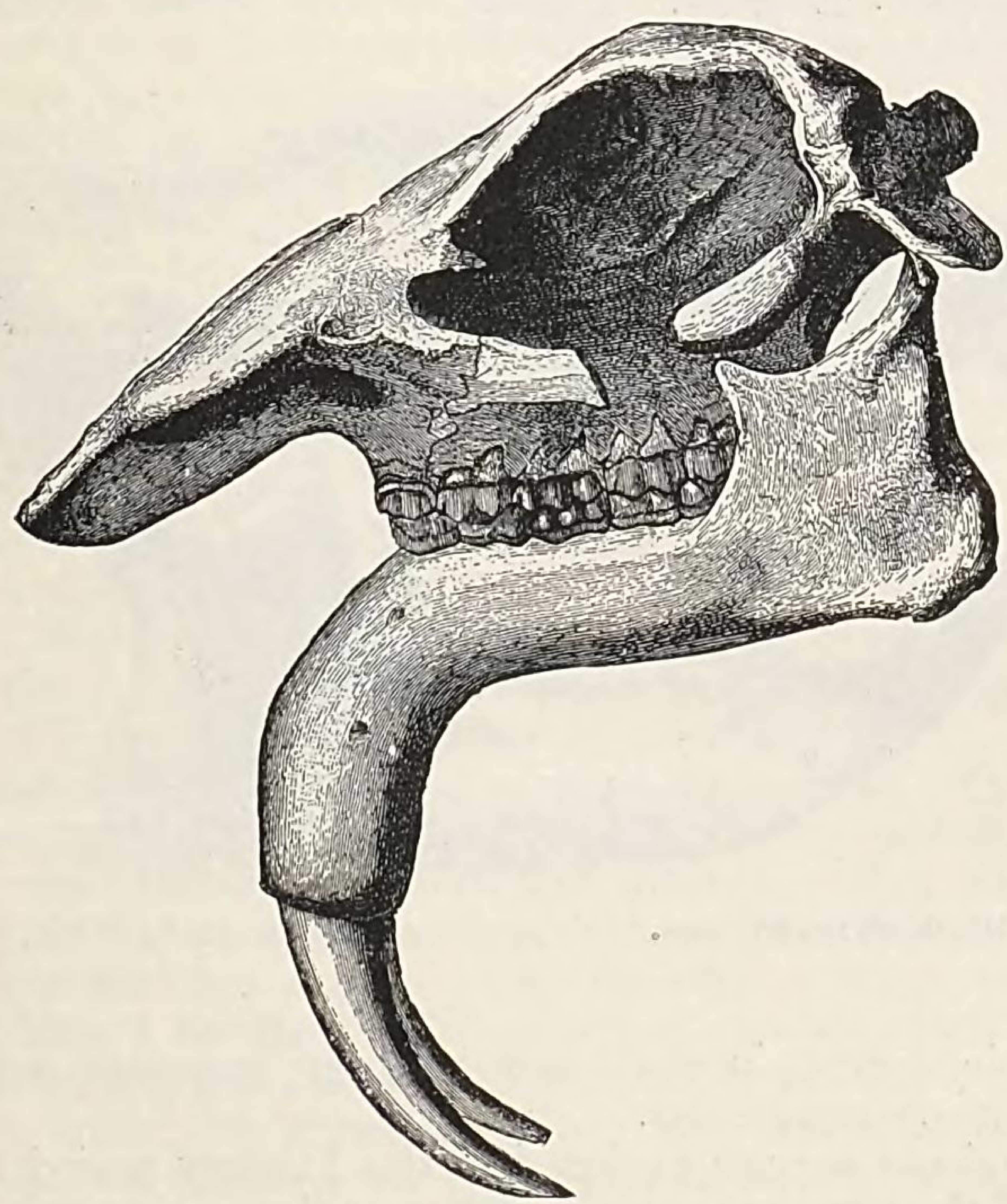


FIG. 1166.—**Dinotherium giganteum.** Side view of skull. $\frac{1}{15}$th natural size. (From Yittel's *Palæontology*, after Kaup.)

the calcaneum. The feet are short, pentadactyle, and plantigrade. Canines are present in both upper and lower jaw; the pre-molars and molars are short and lophodont in type.

Found hitherto only in the Patagonian lower Tertiary (Upper Cretaceous?) formations are two imperfectly known groups of primitive Ungulates, the *Pyrotheria* and *Astrapotheria*.

The true Carnivora of the Tertiary period are, as compared with those of the present time, remarkable for the absence of the well-marked distinction into groups such as are now to be recognised; numerous intermediate forms connect together the Dogs, Civets,

Cats, Bears, and Weasels which, in the existing fauna, appear separated from one another by differences of the most strongly-marked character. Several extinct families are recognised, and one extinct order—the *Creodonta*. The latter present resemblances to the Insectivora on the one hand, and to the Polyprotodont Marsupials on the other, such as would appear to indicate a relationship with both of those groups.

A group of Eocene Mammals of uncertain affinities are the *Tillodontia* (Fig. 1167), which by some have been elevated to the rank of a distinct order. The Tillodontia appear to unite in a

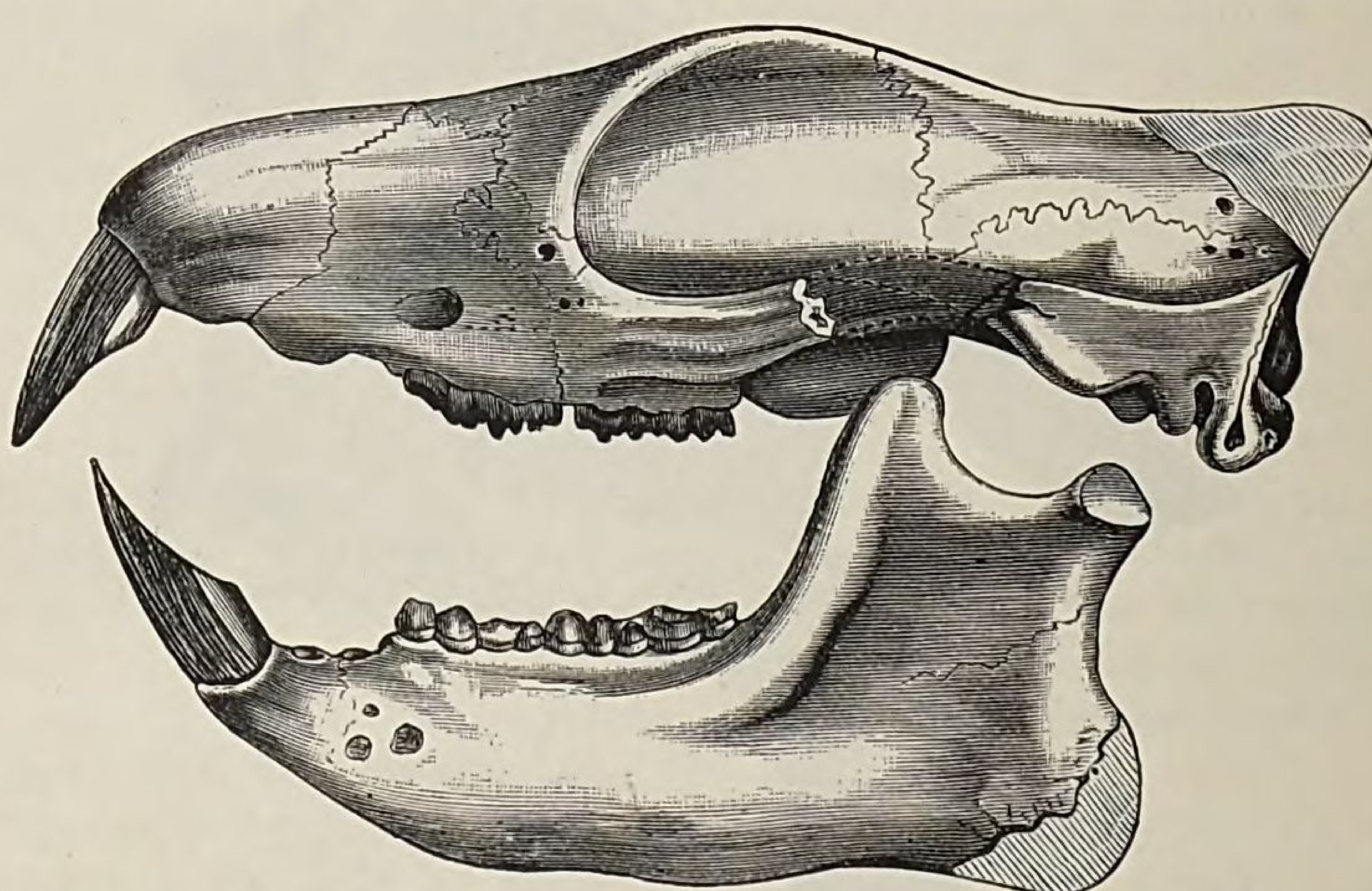


FIG. 1167.—**Tillotherium fodiens.** Left lateral view of skull. (From Flower, after Marsh.)

remarkable degree, in skull and dentition, ungulate, rodent, and carnivorous characteristics.

The Rodents were represented in the Tertiary period by all, or nearly all, the principal groups existing at the present day, together with several extinct families. Some of the Tertiary Rodents attained a much larger size than any living members of the order.

Among the Tertiary Insectivora, in addition to representatives of existing families, are a number of extinct forms. Through these it is possible to connect the living Insectivora with the Creodont Carnivora on the one hand, and with the Prosimii on the other.

Chiroptera, not differing widely from existing forms, occurred as early as the Eocene.

Prosimii occur from the Eocene onwards. A single extinct family is known, comprising Lemuroids which bear a closer resemblance to Insectivora than do the living members of the order. Of the Anthropoidea the Hapalidæ and Cebidæ are only

represented in the Pleistocene of South America; the Cercopithecidæ in the Pliocene and Pleistocene of India by species of the existing genera *Macacus*, *Semnopithecus*, and *Cynocephalus*, and in the Pliocene of India, France, and Italy by species of extinct genera. Among the Simiidæ the Gibbons occur in the Miocene of France and the Pleistocene of Borneo. An extinct genus, *Dryopithecus*, occurring in the Miocene of Europe, is related to the Gorilla; and a species of Orang (*Simia*), together with a form allied to the Chimpanzee, occur in the Indian Pliocene.

The earliest fossil-remains of Man have been found in deposits of Pliocene age in Java; but though flints of undoubted human manufacture have been found in the Miocene of India, evidences of his existence are extremely rare until we reach the Pleistocene.

The Mutual Relationships of the Chordata.

In discussing the relationships of the various groups of Chordata, it will be convenient to begin with Fishes, and to work from them upwards and downwards.

The question of the inter-relationships of the various groups of Fishes is a very puzzling one. As in other cases of the kind, there are three lines of evidence to be kept in mind, anatomical, embryological, and palæontological, the last being always, when available, the final court of appeal.

With regard to anatomical evidence it seems fairly obvious that Fishes having neither limbs nor jaws are more primitive than forms in which those structures are present, unless undoubted evidence of degeneration can be produced: that a purely cartilaginous skeleton is more primitive than a bony one, and a notochord than a vertebral column, however simple; that a brain with distinct cerebral hemispheres is more advanced than one having an undivided prosencephalon; that an autostylic skull, being due to the concrescence of originally distinct parts, is more specialised than a hyostylic skull; that the loss of the spiracle and the presence of an operculum and of a highly differentiated hyoid arch are evidences of specialisation, as also are the presence of air-bladder or lung, spiral valve, conus arteriosus, or copulatory organs.

In embryology, eggs with much food-yolk are to be looked upon as more modified than those with little, unless there is distinct evidence of reversion towards an alecithal condition. Any special contrivances for the nourishment and protection of the embryo, obviating the necessity for the production of immense numbers of eggs, are also marks of advance.

On both these lines of evidence the lowest place may safely be assigned to the Cyclostomes. In spite of the similarity of the

lateral cartilage of the Lamprey to Meckel's cartilage, and of a pair of low ridges at the sides of the anus to vestigial lateral fins, there is no real evidence that the ancestors of the class had either jaws or limbs, and the most reasonable theory is that they are the descendants—highly specialised in certain respects in accordance with their peculiar mode of life—of a primitive craniate stock.

With regard to the two largest groups of Pisces—the Elasmobranchii and the Teleostei—the evidence from anatomy and embryology is conflicting. The Teleostei take the highest place in virtue of their skeleton, operculum, air-bladder, and gills, as well as in their extraordinary adaptability to various environments, but the Elasmobranchs reach a distinctly higher grade of organisation in their enteric canal, heart, brain, and urinogenital organs, as well as in their large and well protected eggs. The anatomy of Ganoids seems to show, however, that the spiral valve, conus arteriosus, cerebral hemispheres, and typical oviducts (Müllerian ducts) have been lost in the course of the evolution of the Teleostei, and that the simpler structure of these organs in that order is actually a concomitant of their extreme specialisation.

The Holocephali and the Dipnoi, while agreeing with Elasmobranchs in many important respects, show an advance in the presence of an autostylic skull and of an operculum, while the Dipnoi rise above all other Fishes in possessing lungs, posterior nares, and a partially divided auricle. The lung appears to have been derived from an air-bladder with pneumatic duct opening on the ventral wall of the pharynx, as in Polypterus; by the dorsal shifting of the duct and its final atrophy the closed air-bladder of the higher Teleostei has arisen.

Coming to the results of Palæontology, many striking and unexpected facts have recently come to light. There is reason to believe that Palæospondylus is a Cyclostome, but one with well-developed vertebræ, from which it must be assumed either that the vertebral column of existing members of the class is degenerate, or that Palæospondylus is a highly specialised offshoot of the primitive Cyclostome stock, in which a vertebral column had been independently acquired. The latter conclusion seems the more probable, and is supported by the fact that in all three orders of Ganoids there are some species with a persistent notochord, others with well-ossified vertebræ, the conclusion being that the vertebral column is a polyphyletic structure, that is, has been evolved independently in various groups in accordance with similar conditions.

Among extinct Elasmobranchs the Acanthodea and Pleuracanthea had membrane bones investing the cranium, and Cladoselache had no claspers. These facts seem to indicate as a probable ancestor of the Teleostomi and Dipnoi—the two sub-classes with

ossified skeleton—a generalized Elasmobranch in which fusion of dermal ossicles into membrane bones had begun, but in which the special reproductive phenomena of the existing members of the group—internal impregnation and few, large, well-protected eggs —had not yet been acquired. The origin of the Dipnoi from such a source is rendered more probable by the possession of the characteristic biserial fin or archipterygium by Pleuracanthus. The Holocephali and the existing Elasmobranchs may be considered as having arisen from the same primitive stock along diverging lines of descent, There is, however, at present no evidence to trace or to explain the fusion of the palato-quadrate with the cranium to form the characteristic autostylic skull of the Holocephali and Dipnoi.

The connection of the Ostracodermi with the better-known groups of Fishes is very uncertain. It has been proposed to class them with Cyclostomata on account of the absence—as far as our present knowledge goes—of jaws and limbs, and attempts have been made to show affinities with the Xiphosura and with larval Tunicates. They seem, however, to be undoubted Fishes, but with no clear relationship to any existing group. The Arthrodira appear to be most closely allied to the Dipnoi.

The question of the origin of Fishes from lower forms is involved in the greatest obscurity. Practically the only assistance in the solution of the problem is furnished by Amphioxus, which seems to indicate as the ancestral stock of Vertebrates, fish-like animals having a skeleton in the form of a notochord, fin-rays, buccal cartilages, and branchial rods; a barely differentiated brain; no heart, but a contractile ventral vessel below the pharynx and a dorsal vessel immediately beneath the notochord; colourless blood; distinct nephridia; a cœlome developed as an enterocœle; metamerically arranged gonads devoid of ducts; and alecithal eggs. The forward extension of the notochord, the immense pharynx, the very numerous gill-slits, and the atrium, are very probably characters special to the Acrania; but even putting them aside as of no phylogenetic importance, it is obvious that this class must have sprung from a point very low down the chordate stem. The morphological differences between Amphioxus and a Hag are, in fact, of a more fundamental character than those between a Hag and a Mammal.

Still lower must have been the point of origin of the Urochorda, with the notochord confined to the tail, the dorsal mouth, and the absence of myomeres and of nephridia. The huge pharynx with its innumerable stigmata is undoubtedly a secondary character; but the atrium, endostyle, dorsal lamina, and peripharyngeal bands seem undoubtedly to indicate an affinity with the Acrania. So also do the earlier stages of development, but the later stages, and especially the mode of origin of the atrium, are quite different in the two cases.

The propriety of including the Adelochorda among the Chordata is still *sub judice.* Allowing that any single organ may have a polyphyletic origin, *i.e.*, may arise independently in different groups in accordance with similar needs, it seems highly improbable that three such peculiar and characteristic structures as notochord, hollow dorsal nervous system, and gill-slits, can have arisen together more than once in the history of animals, and if it could be shown with certainty that these three characters were all present in the Adelochorda their place in the chordate phylum would be assured. But the cavity or cavities in the dorsal nerve-cord of Balanoglossus are inconstant, and are very different from the neurocœle of Urochorda and Vertebrata, which extends, from the first, through the whole length of a well-defined dorsal nervous system. In Cephalodiscus and Rhabdopleura, moreover, there is no trace of any such cavity.

The pharyngeal diverticulum of the Adelochorda, also, is a very different thing from the notochord of Urochorda and Vertebrata, which is formed as a rod separated from the entire mid-dorsal region of the mesenteron, nothing in its structure or development giving the slightest indication that it originally arose as a forward outgrowth of the anterior portion of the mid-gut. The diverticulum of Adelochorda is, in fact, obviously a support to the persistent prostomium of a fixed or sluggish animal, while that of Urochorda and Vertebrata forms a strengthening axis, either to the tail alone or to the whole body, of an active, elongated, animal, swimming by lateral movements of the tail; and there seems to be no reason why two such different structures should not have had an independent orgin. The supposed double "notochord" of Actinotrocha, the larva of Phoronis, is even more problematical.

Far more significant are the gill-slits, but even their evidence is hardly conclusive, since they are absent in Rhabdopleura and Actinotrocha, and in Cephalodiscus are a single pair of apertures, having apparently no respiratory function. In Balanoglossus, however, they are very numerous and increase in number with the growth of the animal, as in Amphioxus, and the division of each by a "tongue" is very similar in the two cases. Further homologies have been suggested by comparing the snout of Amphioxus with the proboscis or pre-oral lobe of Adelochorda and its pre-oral pit with the proboscis-pore.

On the whole, although it is by no means certain that the "chordate" peculiarities of the Adelochorda may not have been independently evolved, it is convenient to retain them in the present phylum, pending further knowledge of their true affinities.

By various zoologists the Chordata have been supposed to be derived from Nemertinea, from Chætopoda, and from Arthropoda. In the Nemertinea the proboscis sheath has been compared with the notochord and the proboscis itself with the pituitary invagina-

tion. Chætopods have been compared with inverted Vertebrates the ventral nerve-cord being homologised with the neuron ; the metameric muscular, circulatory, and excretory systems lend support to this view. Elaborate comparisons have been instituted between the brain of Cyclostomes and Fishes and those of Crustacea and Xiphosura, and it has been sought to explain the neurocœle as the discarded Arthropod enteric canal. But if Amphioxus and the Urochorda, to say nothing of the Adelochorda, are branches from some low part of the chordate stem—a fact it seems hardly possible to doubt—it is obvious that there can be no direct connection with the highly specialised classes referred to. If, for instance, the lower Craniata sprang either from a Chætopod-like or from a Limulus-like ancestor, Amphioxus and the Tunicates must either have no connection at all with Vertebrates, or must have undergone a quite inconceivable amount of degeneration.

As far as we can see, Amphioxus and the Urochorda show not the slightest approach to any other phylum ; Balanoglossus has certain affinities with Echinoderms ; Rhabdopleura and Cephalodiscus are in some respects related to, and were formerly classed with, the Polyzoa Ectoprocta ; Phoronis has been assigned both to the Polyzoa and to the Gephyrea. On the whole it may safely be said that the ancestry of Vertebrates is still an unsolved problem.

With regard to the higher classes, Amphibians may be held to have arisen from a Fish-type allied to the Dipnoi, the resemblances of which to the Amphibia are so great as to lead some authors to place them in a distinct class intermediate between Fishes and Amphibia. The chief difficulty in this case—and it is a serious one—is the derivation of the pentadactyle limb from the Fish's fin, a transformation of which no satisfactory explanation is at present offered either by anatomy, embryology, or palæontology.

Reptiles may be considered to have arisen from a generalised amphibian stock, but there is no direct evidence on this point, and, apart from purely theoretical considerations, there is nothing to show how or why gills vanished so completely as to leave no trace of their existence beyond the branchial clefts, or by what steps the allantoic bladder became precociously enlarged into an embryonic respiratory organ. The precise mode in which the protecting amnion arose is also very doubtful, but from theoretical considerations its development in the Hedgehog (p. 560) seems to indicate a more primitive condition than obtains in the other Mammalia or even in Sauropsida.

Birds appear to be undoubtedly derived from true Reptiles, although nothing is known of the actual ancestral form. In spite of the enormous adaptive differences between the warm-blooded, feathered, bipedal Bird, and the cold-blooded, scaly, quadrupedal Reptile, the connection between the two is far closer than between any other two vertebrate classes.

Mammals also appear to have had a reptilian origin; the numerous reptilian characters of the Monotremata certainly point in this direction, and the reproductive processes of that group and of the Marsupials help us to understand the stages by which the large-yolked egg of the ancestral form, developed outside the body, gave place to the secondarily alecithal egg of the typical Mammal, developed within the uterus, and nourished by a complete placenta.

The following diagram may serve as a rough illustration of the views set forth in the preceding pages—

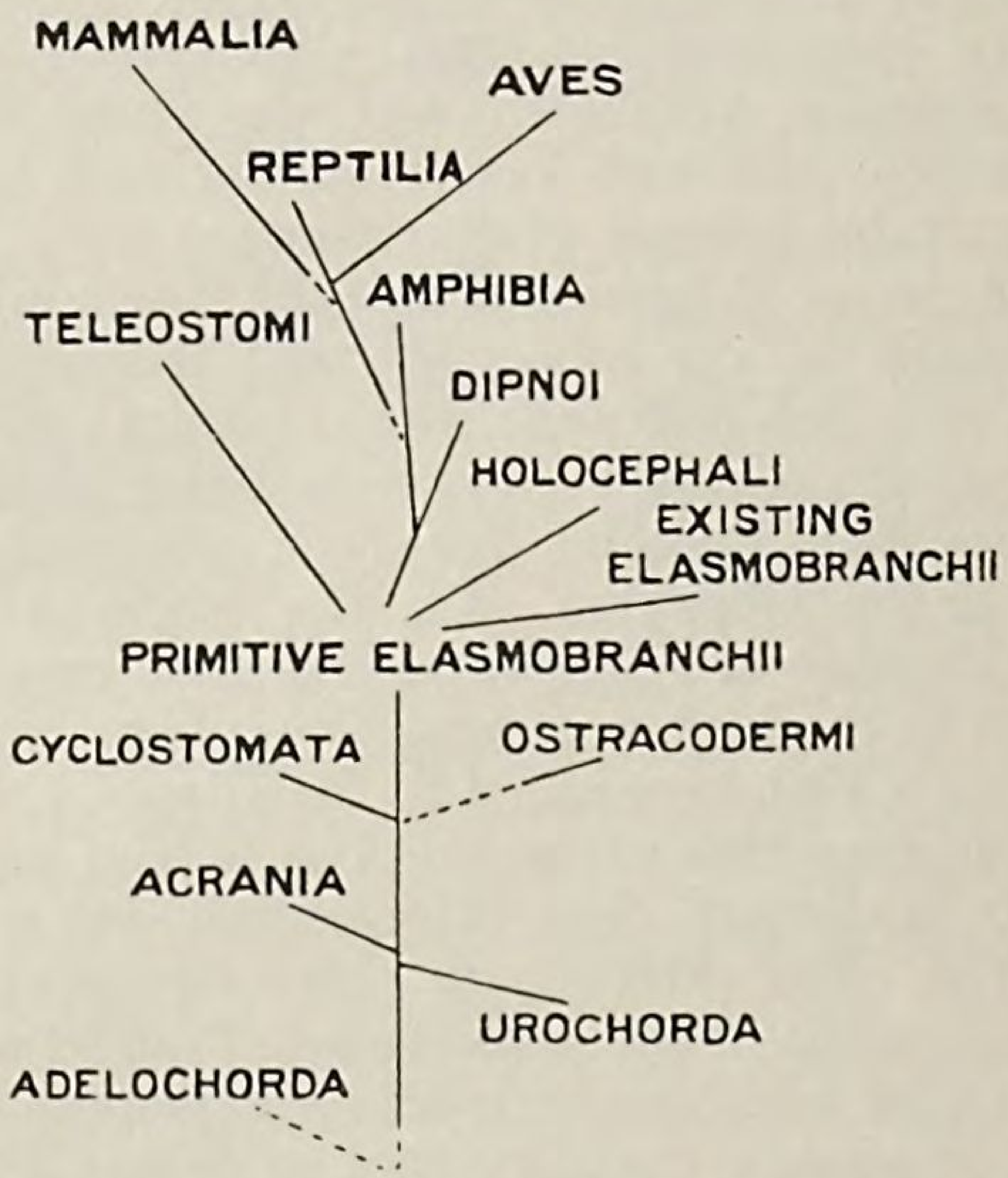


FIG. 1168.—Diagram illustrating the Mutual Relationships of the Phyla of Animals.

On the Mutual Relations of the Phyla of Animals.

It will be advantageous in concluding our survey of the animal kingdom to sum up with a few remarks as to the phylogeny of the primary groups or phyla, since that of the sub-divisions of each phylum has already, in nearly every case, been discussed.

It cannot be too strongly insisted upon that in the majority of cases it is useless to seek for the ancestors of any animal among existing forms. As far as we know, most living species are culminations—terminal branches of the great tree, not leading directly to any other form, but connected only at the fork of a branch. It is, as a rule, only among fossils that actual ancestral forms are to be looked for; hence the area of strict phylogenetic investigation is very limited, and in the majority of cases the only evidence is to be sought in anatomy and embryology.

Not only are most existing species culminations and therefore off the direct line of ancestry of other species, but, as far as we can judge, the same is true of most genera and families, of a large majority of orders and classes, and even of most phyla. It would certainly seem that existing Chordata, Mollusca, Arthropoda, Annulata, Echinodermata, Nemathelminthes, and Platyhelminthes are all independent branches of the animal tree, having no connection with one another save through the trunk.

There are, however, existing groups which seem to represent actual stages in the existence of others. For instance, it can hardly be doubted that Amphibia are derived from Fishes and Birds from Reptiles; that if we could discover the unknown ancestors of those classes they would be classed definitely among Pisces and Reptilia respectively, though probably not belonging to any known order.

In the same way everything seems to point to the conclusion that all the higher phyla must have passed through some kind of cœlenterate stage, and, before that, some kind of protozoan stage, so that these two phyla may be said to represent actual steps in the evolution of the higher forms. It is therefore legitimate to assume, in the absence of direct evidence, that the ancestors of both the Cœlenterata and the Porifera were unicellular or non-cellular forms, *i.e.*, to be classed among the Protozoa, and that the ancestors of the nine higher or triploblastic phyla were diploblastic forms, *i.e.*, to be classed among the Cœlenterata.

Most, if not all, of the triploblastic phyla appear to be terminal or culminating groups. There is no reason for thinking that either of the three highest phyla—the Chordata, Mollusca, and Arthropoda—ever passed through a stage which, if known, would be classed among Platyhelminthes, Nemathelminthes, Echinodermata or Annulata. The wide occurrence of the trochosphere or some similar larval form seems, however, to indicate a certain bond of union. The typical trochosphere of Annulata and Mollusca, the echinopædium of Echinoderms, the ciliated larva of Molluscoida, the tornaria of Balanoglossus, and the adult Rotifer, present, amid endless diversity in detail, common characters which, in the absence of better evidence, may be considered as indications of remote affinity. The Arthropoda alone among the higher phyla are devoid of even this slender connection with lower forms; there is no indication throughout the phylum of anything approaching to a trochosphere, the crustacean nauplius is quite *sui generis*, and the larval forms of Insects and Arachnids simply suggest a homonomously segmented ancestor. This suggestion is supported by Peripatus, the cilia, true cœlome, nephridia, and ladder-like nervous system of which certainly point to its derivation from a segmented "worm" not far removed from the annulate type.

In accordance with these conclusions the mutual relationships of the phyla may be expressed in a diagrammatic form as follows:—

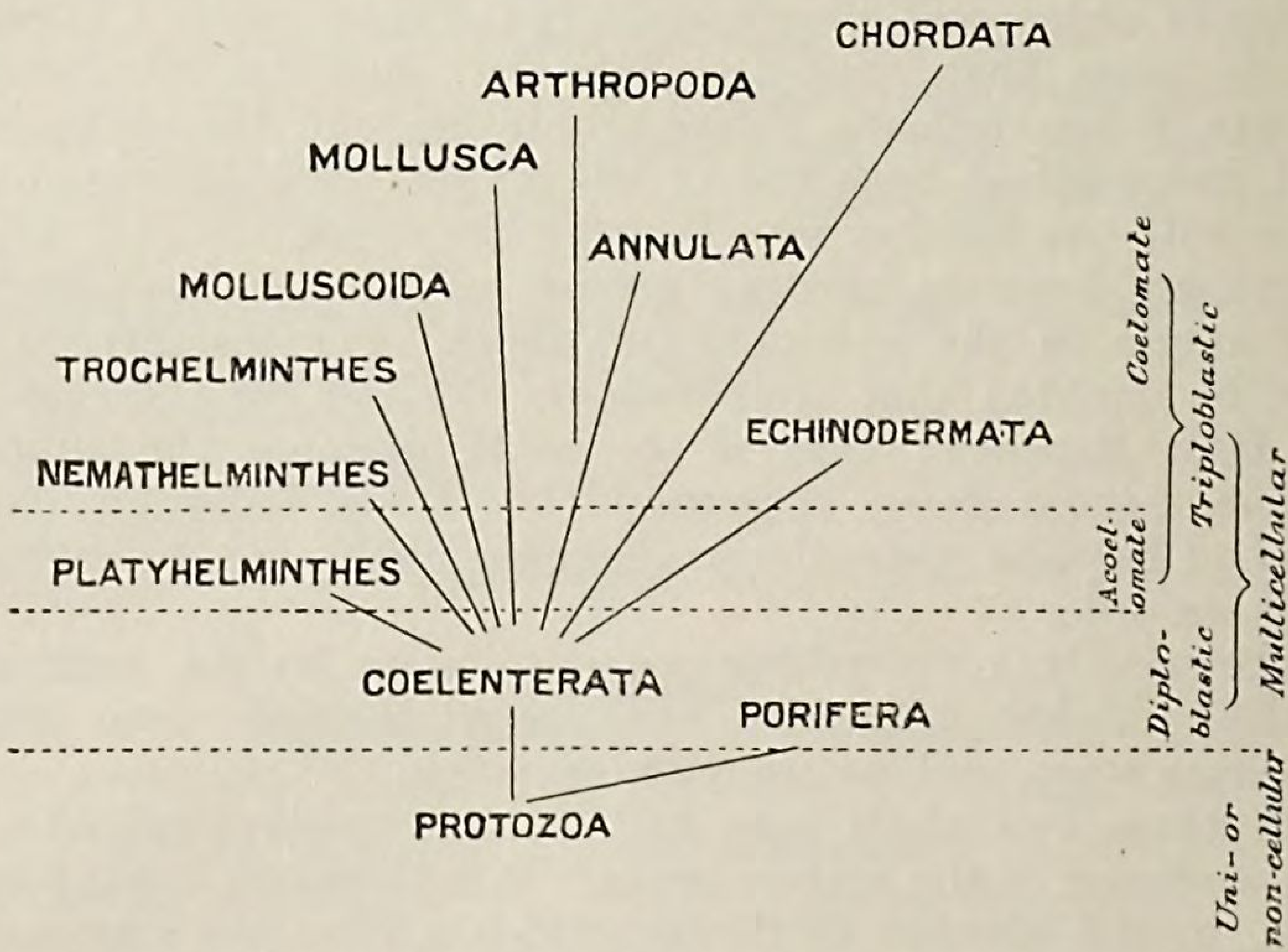


FIG. 1169.—Diagram illustrating the Mutual Relationships of the Chordata.

SECTION XIV

DISTRIBUTION

In discussing the various groups of animals, the subject of their geographical and geological distribution has in every case been referred to, and the reader will already have noticed how strikingly the different parts of the earth's surface at the present day, and the different periods of its geological history, differ from one another in respect of their animal inhabitants. In order to bring forward the facts of distribution more prominently, the present section will be devoted to this important subject.

1. Geographical Distribution

The facts and ideas of which the subject of Geographical Distribution takes cognizance are clearly brought out by comparing the fauna of Great Britain with that of the most distant of her colonies, New Zealand, including, in each case, the adjacent islands. The two countries are not widely different in size. The climate of each is temperate, Great Britain extending from about 50° to 60° north latitude, and having a mean annual temperature of about 48° F., New Zealand extending from about 34° to 48° south latitude, and having a mean annual temperature of 55°. Both contain mountainous regions, forests, and arable land. The climate of both is humid, the rainfall of Great Britain being from about 25 to 30 inches in flat, 40 to 80 inches or more in mountainous districts, while the average rainfall for the whole of New Zealand is about 50 to 55 inches. The physical conditions of the two countries are thus very similar, the chief differences being the far higher summer temperature of the northern part of New Zealand, and the far lower winter temperature of the northern part o Great Britain.

But when we come to compare the faunæ of the two countries these similarities disappear. In Great Britain there are about

forty species of native land Mammals, including Ungulata (Wild Cattle, Red Deer, Fallow Deer, &c.), Carnivora (Fox, Badger, Wild Cat, Stoat, Marten, &c.), Rodentia (Squirrel, Rabbit, Hare, &c.), Insectivora (Hedgehog, Shrew, and Mole), and twelve species of Bats. Moreover, within the historic period, the Wolf, Bear, Wild Boar, Reindeer, and Beaver were among the wild animals of Britain.

In New Zealand, on the other hand, the only land Mammals found in the islands previous to the advent of Europeans were two species of Bats (*Chalinolobus morio* and *Mystacina tuberculata*), the Maori Dog, which was certainly introduced by the Maories who colonised New Zealand from some of the Pacific Islands not many centuries ago, and the Maori Rat (*Mus maorum*), which perhaps owes its introduction to the same source. With the exception, then, of Seals; two Bats, and perhaps a Rat, are the only native Mammals of New Zealand.

The Birds of the two countries also offer a marked contrast. Great Britain has no native Ratitæ; in New Zealand there are now living five species of Apteryx, while within the historic period—three or four hundred years ago or less—there lived in the two islands half-a-dozen genera, and some five-and-twenty species of Moas (Dinornithidæ). Great Britain has no Parrots; New Zealand has two species of *Nestor*, three Parrakeets of the genus *Platycercus*, and the extraordinary Ground Parrot or Kakapo (*Stringops*). On the other hand, the Finches (Fringillidæ) are wholly absent in New Zealand, but abundantly represented in Great Britain. Moreover, New Zealand is remarkable for the large number of flightless Birds included in its fauna: besides the Kiwis and Moas, there are *Stringops* (Ground Parrot); *Ocydromus*, *Cabalus*, and *Notornis* (Rallidæ); *Nesonetta* (the flightless Duck of the Auckland Islands); besides the extinct Giant Goose (*Cnemiornis*) and Giant Rail (*Aptornis*). In Great Britain none of the Birds are actually flightless.

As to Reptiles the difference is less striking, but is still sufficiently marked, the most important facts being the entire absence of Snakes in New Zealand and the presence of Hatteria, the only existing representation of the Rhynchocephalia. Lizards occur in both countries, and in both Crocodilia are wholly absent, and Chelonia occur only as occasional visitants.

Great Britain possess four species of Tailed Amphibia (Newts), and the same number of Frogs and Toads. In New Zealand Urodeles are entirely absent, and there is only a single and rare species of Frog (*Liopelma hochstetteri*).

The fresh-water Fishes of Britain are numerous and varied; the most important are the various species of Salmo (Salmon and Trout), the Perch, Carp, Grayling, Pike, Eels, &c. In New Zealand there are only Eels, a small salmonoid, *Retropinna*, not found else-

where, and several species of *Galaxias*, an exclusively Australasian, South African, and South American Physostome The differences between the marine Fishes, though obvious enough, are less fundamental, a fair proportion of the New Zealand shore-fishes belonging to the same families, and in some cases even to the same genera and species, as those of Britain.

Among Mollusca the fresh-water *Unio* (fresh-water Mussel), are found in both countries, but New Zealand has no species of the common genus *Helix* (Land-snail), abundant in Great Britain, and its molluscan fauna generally is very peculiar.

The Insect-fauna of New Zealand is remarkable for the paucity of Butterflies—fifteen species against about seventy in Britain—and for the abundance of Moths, mostly belonging to the Micro-lepidoptera and the Geometrina. The occurrence of Peripatus in New Zealand furnishes another strong point of contrast. Amongst fresh-water Crustacea the British *Astacus* is represented by an allied genus *Paranephrops*. Among marine Crustacea many genera are common to the two countries, but there are numerous peculiar forms, and it is worthy of mention that the New Zealand species of Palinurus belongs to a more generalized type than the British species, having no stridulating organ.

The British Earthworms all belong to the familiar *Lumbricidæ* (including *Lumbricus*) and *Cryptodrilidæ;* in New Zealand both these families are absent, and the majority of the Earthworms belong to the *Acanthodrilidæ*, including the genera *Acanthodrilus*, *Octochætus*, &c. Lastly, there are found in New Zealand at least twenty species of Land Planarians and one terrestrial Nemertean; neither of these groups is represented in the land-fauna of Britain.

That these striking differences are quite independent of climate, food, &c.; in other words, that the environment in the one country is in no way inimical to the fauna of the other, is shown by the zoological history of New Zealand since its colonisation. Apart from domestic animals, the Brown Rat (*Mus decumanus*) and the House Mouse (*Mus domesticus*) are now as common in New Zealand as in Britain; the Rabbit has become a plague, barely kept in check by constant effort stimulated by severe legislative enactments; Deer flourish as well in the mountains of Otago as in those of Scotland; the Birds first noticed by a visitor to the settled districts of the colony will probably be the Sparrow, Blackbird, Thrush, Starling, and Goldfinch; and Trout have become so thoroughly acclimatised in the streams and lakes, that in some districts the poorer settlers, like the British apprentices of old, decline to eat them. We thus learn to distinguish between the native or *indigenous fauna* of a country, and the *introduced fauna* which owes its existence to human agency; in comparing the

faunæ of any two countries, the latter element must of course be carefully eliminated.

The contrast between our two selected countries is further emphasised when we compare the fauna of each with that of the nearest continental area, the fauna of Great Britain with that of the continent of Europe, the fauna of New Zealand with that of Australia.

With the exception of the Red Grouse (*Lagopus scoticus*) perhaps the Coal Tit (*Parus britannicus*) and the Long-tailed Tit (*Parus rosea*), and some fifteen species of fresh-water Fishes, the British vertebrates are all found on the European Continent. On the other hand, there are many European species of Mammals, Birds, Reptiles, Amphibia, and Fishes, which do not occur in Great Britain. The British fauna may, in fact, be described as an isolated and somewhat impoverished section of the general European fauna.

Now contrast New Zealand with Australia. Of the two New Zealand Bats, one (*Chalinolobus morio*) occurs also in Australia, the other (*Mystacina tuberculata*) is *endemic*, that is, found nowhere else. Australia, instead of having a Mammalian fauna comprising only two Bats and a doubtful Rat, possesses a large number of characteristic Mammals, all except the Bats, Rats, and Mice, and the Dingo (*Canis dingo*) being either Monotremes or Marsupials. Out of about 200 species of New Zealand Birds, fully 100 are endemic; of the rest only about 50 are found in Australia. Conversely, Australia has a large number of characteristic Birds, belonging to families wholly unrepresented in New Zealand, such as the Birds of Paradise and Bower Birds (*Paradiseidæ*), Cockatoos (*Cacatuidæ*), Mound-makers (*Megapodiidæ*), the Lyre Bird (*Menura*), the Emu, and the Cassowary. Among Reptiles, Hatteria, *i.e.*, the entire order Rhynchocephalia, is endemic in New Zealand, as also is the little Gecko *Naultinus*, while a small genus of Lizards, *Lygosoma*, is common to the two countries. Australia, on the other hand, besides possessing a large number of Lizards, such as the Monitors, is remarkable for the great number of its Snakes, a group quite unrepresented in New Zealand, and has two species of Crocodiles and several of Chelonia. Among Fishes, the presence of Ceratodus in Australia is specially remarkable. The fresh-water Crayfishes of each country are endemic, those of New Zealand belonging to the genus *Paranephrops*, those of Australia to *Astacopsis* and *Engæus*. The majority of the Australian Earthworms belong to the families *Perichætidæ* and *Cryptodrilidæ*, the latter including the Giant Earthworm of Gippsland (*Megascolides*); the Acanthodrilidæ are represented, but are not dominant as in New Zealand.

Thus, while the zoological resemblances between Great Britain and the Continent of Europe are so close as almost to amount to

identity, there is more difference, zoologically speaking, between New Zealand and Australia than between Europe and North America or between England and Japan.

The reason of this remarkable contrast is not far to seek. Geologically speaking Great Britain is a recently detached portion

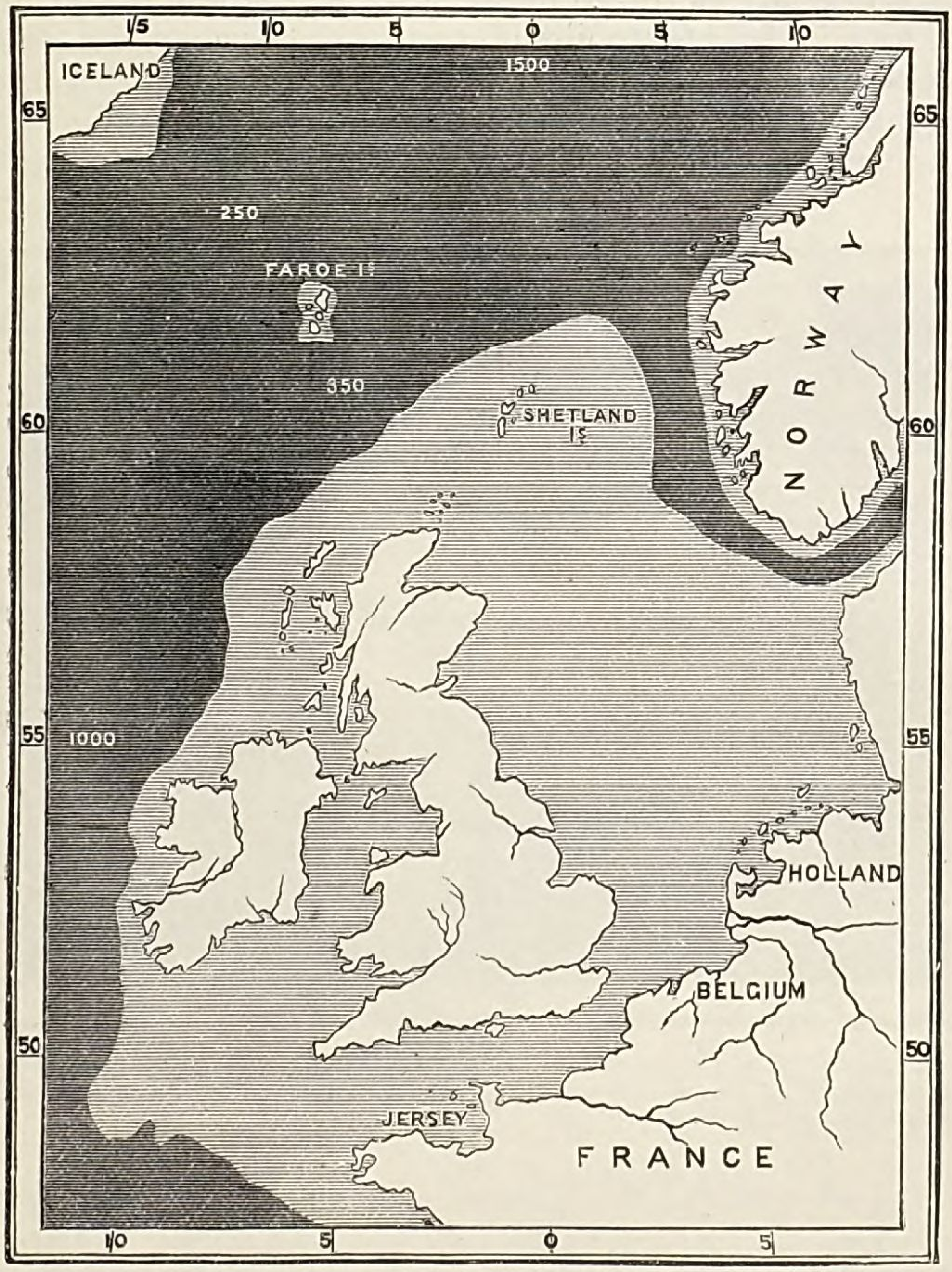


FIG. 1170.—Map showing the shallow bank connecting the British Isles with the continent. The light tint indicates a depth of less than 100 fathoms; the figures show the depth in fathoms. (From Wallace.)

of Europe, having been united with it during the latter part of the Glacial period (Pleistocene), and, at the present moment, an elevation of the bed of the English Channel to the amount of 260 feet, would bring about a re-union (Fig. 1170). Prior to this union, moreover, it was largely submerged so as to leave no trace

of its pliocene fauna. Thus, the British animals are all migrants from Europe, isolated by the post-glacial separation from Europe, and the absence of certain European forms is due to the fact that the separation took place too early to allow of complete migration.

New Zealand, on the other hand, instead of being separated from the nearest Continent by 21 miles of shallow sea, is divided from Australia by 1,000 miles of ocean—the Tasman Sea—varying from 2,000 to 2,600 fathoms (12,000–15,600 feet) in depth. It is almost certain that there was never any direct connection between the two countries, and the only indication of even an indirect con-

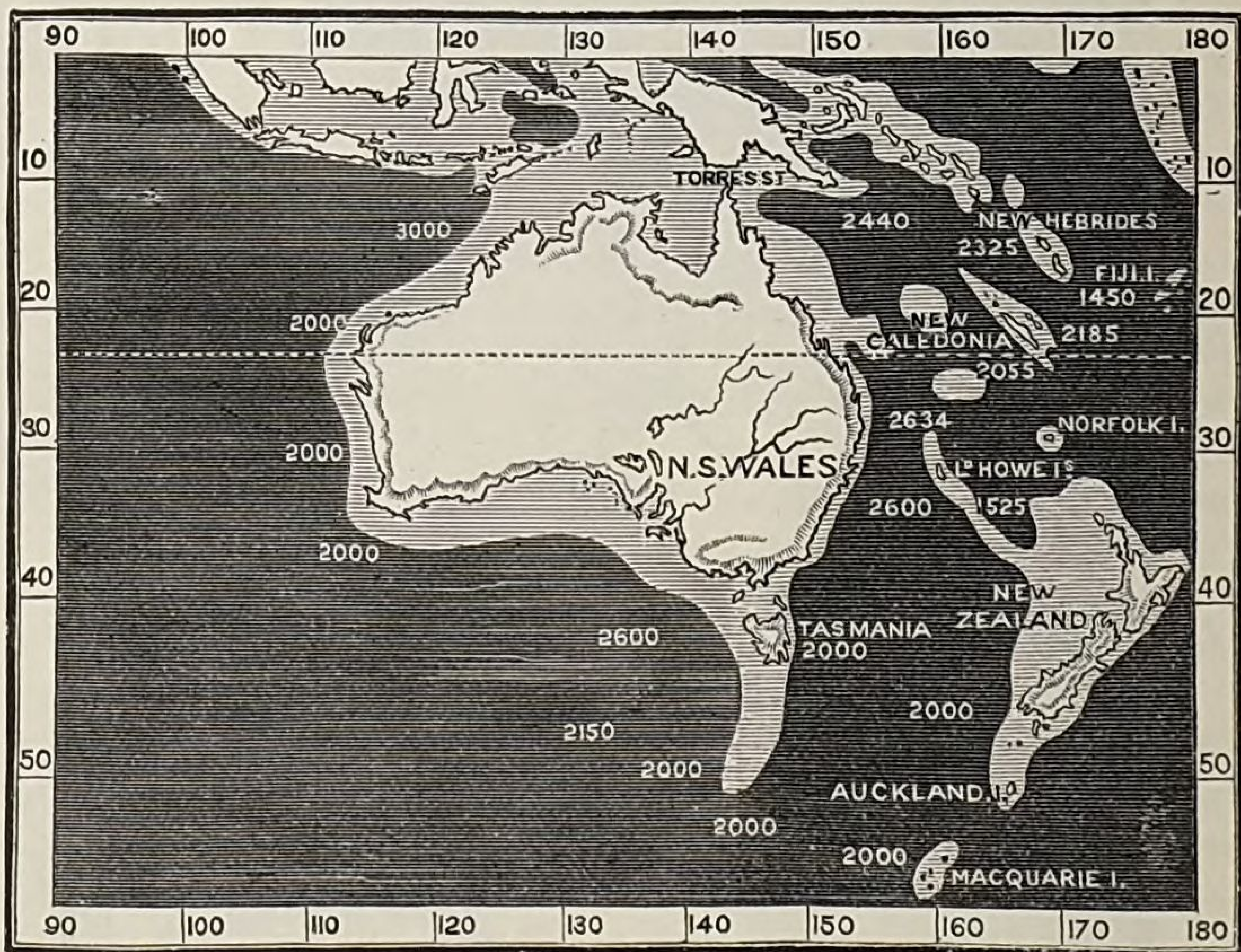


FIG. 1171.—Map showing depths of sea around Australia and New Zealand. The light tint indicates a depth of less than 1,000 fathoms; the dark tint indicates a depth of more than 1,000 fathoms. (From Wallace.)

nection is afforded by the existence of an area of comparatively shallow sea—*i.e.*, under 1,000 fathoms—stretching between the North Island of New Zealand on the one hand, and Northern Australia and New Guinea on the other (Fig. 1171). It would take, therefore, an upheaval of over 6,000 feet to join the two countries, and it may be taken as certain that if there ever was a direct connection, either by continuous land or by a chain of islands, such connection could not have been later than the early part of the mesozoic era.

It must also be noted that while the British fauna is related exclusively to that of Europe, the New Zealand fauna presents not

only Australian but also Polynesian and South American affinities. Some of the Birds are represented by the same or closely allied species in New Caledonia, while the land Molluscs and Insects, the Fresh-water Lamprey (*Geotria*), and the Earthworms show South American affinities. Still more remarkable is the fact that a little fresh-water Fish, *Galaxias attenuatus*, occurs not only in New Zealand and Tasmania, but in the southern extremity of South America and in the Falkland Islands. In this connection it is interesting to find that there is a submerged bank of less depth than the surrounding ocean—under 2,000 fathoms—passing westwards from South America, and including many of the Pacific Islands; and an area, also of less than 2,000 fathoms, in the Antarctic Ocean, sending offshoots northwards. The first of these may possibly indicate a former westward extension of South America, the second a former Antarctic land-area, perhaps more or less directly connected with the existing southern continents. The whole question is quite unsettled and extremely obscure, and is complicated by the fact that in one respect the New Zealand fauna shows Ethiopian affinities. There have lately been discovered in the Chatham Islands, a small group about 400 miles to the east of New Zealand, the remains of a long-beaked Rail (*Diaphorapteryx*), evidently not long extinct, the nearest ally of which is the Red Bird (*Aphanapteryx*) of Mauritius, known to have been exterminated by human agency. Moreover, the great Ratite Birds, the Æpyornithidæ, of Madagascar, show undoubted affinities with the Dinornithidæ.

The foregoing comparison of the faunas of Great Britain and New Zealand leads us to the consideration of certain fundamental conceptions of zoo-geography.

Insular Faunas.—We notice in the first place the striking contrast between the fauna of an island which has been recently detached from a great continental area, and that of an island which has remained isolated for an immense and unknown period. In the one case the fauna has a strictly continental character, there having been insufficient time for modification since the separation took place. In the other case immigration has taken place from various sources over a vast period of time, during which modification has taken place to a sufficient extent to give rise to new or endemic species.

Habitat, Range, and Station.—Each kind of animal has, as a rule, its own *habitat*, fresh-water in one case, the sea between tide-marks in another, marsh, forest, snow-clad peaks, and so on. A similar habitat may characterise whole genera and even orders. Keeping always to its own habitat, the *range* of an animal may extend over a vast area. The marsh-loving Curlew, for instance, is found all over the world; the Cormorants (*Phalacrocorax*), Gulls,

(*Larus*), some Ducks (*Anas*), &c. are also *cosmopolitan* or world-wide in distribution. On the other hand, the range of a species, genus, or order may be restricted to a single limited district. The genus *Liopelma* (New Zealand Frog) is found only in a small area in the Auckland district; the species *Salmo killinensis* (Loch Killin Charr) occurs only in Loch Killin in Inverness-shire; the Order Rhynchocephalia is confined to New Zealand. The entire range may be broken up, as it were, into a number of *stations*, depending sometimes on habitat, sometimes on unknown causes; the Tuatara, for instance, is found at present only in some half dozen small islets, each of which is a station, while the whole of them constitute the range of the species.

Barriers.—A barrier in zoo-geography implies any permanent obstacle to the dispersal of a species. For instance, the Tasman Sea is an impassable barrier to the passage of most animals between Australia and New Zealand, strong-flying birds being the only species able to cross it. On the other hand, the number of Birds able to pass so narrow a strait as the British Channel is very considerable, while still narrower arms of the sea may be crossed by a large proportion of Mammals, Insects, &c. Thus barriers are of unequal importance according to the particular animals under discussion; wide deserts and lofty snow-covered mountain ranges are impassable to most species; to some even a narrow river or arm of the sea is insuperable.

Means of Dispersal.—Most Mammals and many Reptiles can swim across rivers and arms of the sea if not too broad; thus narrow straits and rivers are of no significance as barriers to the dispersal of many animals. On the other hand, rivers of even moderate breadth are insuperable barriers to Monkeys, which are unable to swim.

Aërial animals can overcome many of the barriers impassable to flightless forms. Birds of strong flight often pass over immense stretches of ocean. For instance, a Cuckoo (*Eudynamis taitensis*) habitually winters in Fiji and other Pacific islands, and spends its summer in New Zealand, traversing the enormous distance of 1,500 miles twice a year. Many Insects also are able to fly great distances, especially when carried by gales.

Mechanical dispersal is an important factor in the case of many animals. Small Crustacea and Molluscs may be carried great distances in the mud adhering to the feet of Birds. Infusoria, the eggs of Rotifers, and other microscopic forms may be transported in the dried condition by wind. Birds and Insects are frequently blown out to sea and carried for immense distances, and Mammals, Reptiles, etc. may be widely distributed by being carried on drift-wood or on floating islands or "rafts," formed of large masses of matted vegetation, such as are often detached by storms in the tropics. Finally, the dispersal of many

fixed or shore-haunting animals is ensured by their free-swimming larvæ.

Importance of the Various Groups of Animals in Zoo-Geography.—In close dependence on the means of dispersal we have the fact that the various groups of animals are of very unequal value in the study of distribution. The greater the facilities for the transport of any species across a given barrier, the less significance will attach to its occcurrence on both sides of the barrier. Conversely, when a species having few or no facilities for dispersal, is found on opposite sides of an important barrier, the natural conclusion is either that the barrier is of comparatively recent formation, and that the two areas separated by it were once, so to speak, in zoological continuity, or that the species in question is a very ancient one, and was widely dispersed at a time when the arrangement of the land-surface was very different from what it is at the present day. For instance, the occurrence of strong-flying Birds, such as Gulls and Cormorants, in widely separated countries, is a fact of no significance in determining the mutual relationships of the faunæ of those countries. But the occurrence of the same species of Fresh-water Crayfish—to which the narrowest arm of the sea is an insuperable barrier—in Great Britain and the European Continent, is explained only by the fact—of which there is independent evidence—that the English Channel is of recent formation. And when we find the various species of Peripatus dotted over the earth's surface in an apparently casual manner, we are forced to the conclusion that this genus must formerly have been very widely and continuously distributed and subsequently exterminated over the greater part of its range; since it is hardly possible to conceive of either the adult or the young of this creature, living in rotten wood in the recesses of the forest, having been transported between Australia and New Zealand, or between Africa and the West Indies.

Speaking generally, then, it may be said that discontinuity in the distribution of a species or other group is evidence of its antiquity. In addition to Peripatus, the Dipnoi and the Tapirs may be mentioned as examples.

It will be seen that terrestrial and fresh-water animals are of more importance, from the point of view of zoo-geography, than marine forms. Among the inhabitants of the sea littoral species are of greater significance than pelagic or abyssal. Amongst land animals those which are unable to swim, and those which cannot survive immersion in salt water, are of more importance than strong swimmers, or than such forms as are able to live for a prolonged period on drift-wood, or in mud attached to the feet of Birds.

In connection with what has been said above about there being no special significance about the distribution of certain strong-

flying Birds, it must be remarked that this is by no means true of migratory Birds. Many British Birds, such as the Swallow, Cuckoo, Swift, &c., spend the summer in England, the winter in South Europe or Africa. One of the New Zealand Cuckoos winters in Australia, the others in Fiji or some other Pacific Islands. Birds capable of such feats of flight might, one would think, soon overspread the globe, yet, as a matter of fact, each species is found to keep strictly to its own definite line of migration, even across 1,000–1,500 miles of sea.

Having now indicated the general character of the facts and problems connected with the subject of zoo-geography, we may proceed to give some account of the **Zoo-geographical Regions** into which the land-surface of the earth is divided (see Fig. 1172). It must be borne in mind that the determination of these regions depends largely upon the classes of animals upon which stress is laid, the peopling of any given portion of the earth by a particular class depending upon the time during which it has been in existence and its means of dispersal. Thus regions, founded upon the distribution of Mollusca will differ from those depending on Reptiles or on Birds. The regions adopted here are mainly founded on the distribution of Birds and Mammals.

The whole of Europe, Africa and Arabia north of the Tropic of Cancer, and the whole of Asia except India, Burmah, Siam, and South-east China, together with Japan, Iceland, the Azores, and the Cape de Verde Islands, are so similar in their animal productions as to form a single division of the earth's surface, called the **Palæarctic Region.** This region is bounded on the north, west, and east by ocean, but its southern limits are at first sight less obvious. It appears strange, for instance, that Northern Africa and Arabia should be included in this region, the Mediterranean being, as it were, ignored as a boundary. But the facts show that the great line of sandy deserts in the region of the Tropic of Cancer, the Sahara in Africa, and Roba el Khali in Arabia, form a far more efficient barrier to the dispersal of species than the Mediterranean, and it is probable that there was direct land connection between Europe and North Africa during the Pleistocene period. In Asia the Himalayas form an effective barrier, which has existed since Tertiary times, between Thibet and India; an ill-defined line of country following the course of the Indus continues the boundary south-west to the shores of the Arabian Sea; and another ill-defined area passing south of the Yang-tse-Kiang, and travelling northward to Shanghai, constitutes the eastern end of the southern boundary of the region.

None of the larger groups of animals, no orders or even families, are absolutely confined to this region, the characteristics of which it is difficult to define without descending to genera and species. The Moles (*Talpidæ*), Sheep and Goats (*Ovidæ*), and Dormice; the

MAP OF THE WORLD DIVIDED INTO ZOO-GEOGRAPHICAL REGIONS.



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Stanford's Geog.l Estab.t London

Pheasants, Robins, Magpies, and many other Birds are highly characteristic, and many species of Deer, Oxen, and Antelopes, Rodents, Passerines and other Birds, Reptiles, Amphibia—including Proteus—and fresh-water Fishes, are endemic.

The Palæarctic region includes, as we have seen, nearly all the northern portion of the eastern hemisphere; the corresponding part of the western hemisphere, viz., North America, with Greenland, constitutes the **Nearctic Region**. It also is bounded by the ocean on its northern, eastern, and western sides, while in the south an ill-defined tract of country, passing between Cape San Lucas on the west and the Rio Grande del Norte on the east, separates it from the Neotropical region.

The Nearctic differs from the Palæarctic region in the possession of several characteristic Mammals, such as Opossums (*Didelphyidæ*), the Skunk, Racoon, etc.; many Birds, such as the Blue-jays, and Turkey-buzzards, etc.; Reptiles, such as Rattlesnakes and Iguanas; Amphibia, including the Axolotl, Necturus, Siren, and other large Urodeles; and numerous fresh-water Fishes, including Amia, Lepidosteus, Polyodon, and Scaphirhynchus. Only three entire families are endemic, two of Rodents, and one of Passerines.

On the other hand, the resemblances between the two northern regions are very close. Both possess Wild Cats, Hyænas, Foxes, Weasels, Bears, Elk, Deer, Wild Oxen, Beavers, Voles, Squirrels, Marmots, and Hares, the species of the one region being all closely allied to, and sometimes identical with, those of the other. Thrushes, Wrens, Tits, and Finches are also common to the two regions, and, generally speaking, the differences between them are, as we shall see, nothing like so striking as those between either of them and the region or regions bounding it to the south. Hence the Palæarctic and Nearctic regions are sometimes grouped together as a single *Holarctic Region.*

In the southern regions the characteristic features are much more striking. The **Ethiopian Region** is constituted by the whole of Africa and Arabia south of the tropic of Cancer, together with Madagascar, Mauritius, Bourbon, Rodriguez, and the Seychelles. The region is bounded by sea on the west, south, and east, but on the north it is perfectly continuous with the Palæarctic region, and it certainly seems a very remarkable fact, until we remember what an impassable barrier is afforded by a sandy desert of great extent, that there should be more difference between the faunæ of northern and central Africa than between those of England and Japan, or of Alaska and Florida.

Among the animals most characteristic of the Ethiopian region and not found elsewhere are the Gorilla, the Chimpanzee, several

Baboons, and the large majority of Lemurs, including the curious Aye-aye (*Chiromys*); several peculiar Insectivora, such as the Golden Moles (*Chrysochloridæ*), and the River Shrew (*Potamogale*); the African Elephant, the Hippopotamus, two or three species of Rhinoceros, the Zebras and Quaggas, and more than seventy species of Antelopes; the Aardvark (*Orycteropus*), one of the most singular types of Edentata; the Plantain-eaters (*Musiphagidæ*), the Secretary Bird (*Serpentarius*), and many other families and genera of Birds; numerous Snakes and other Reptiles, and several fresh-water Fishes, including the Dipnoan *Protopterus*, and the ganoid *Polypterus*. The Lion, Leopard, and Ostrich are also characteristic, although not actually endemic, since the two former extend into the Palæarctic and Oriental regions, while the Ostrich occurs in Arabia and Syria. Almost equally remarkable are the negative peculiarities of the region, and especially the absence of Bears, Deer, and Oxen, and the extreme paucity of Goats, Sheep, true Pigs (*Sus*) and Shrews.

The great island of Madagascar is characterised by the immense number of Lemurs, the absence of Monkeys, and the poverty of its carnivorous and ungulate fauna, the Lions, Antelopes, etc., of the African continent being all absent. Most of its Mammals are endemic, only three out of twenty-eight (including Bats) being found in Africa. The Birds also are quite different from those of the African continent. It shows affinities with America in the presence of a peculiar family of Insectivora (*Centetidæ*), otherwise found only in the West Indies, and of certain Snakes; and its relationships with India are so marked that it has been proposed to account for them by assuming the former existence of a land connection, in Jurassic and Cretaceous times, extending north-eastward across the Indian Ocean and represented at the present day by the Seychelles and other neighbouring islands. In the opinion of some authorities these peculiarities entitle Madagascar and the adjacent islands to rank as a distinct zoo-geographical region.

The **Oriental Region** consists of India, Burmah, Siam, south-eastern China, and certain islands of the East Indian Archipelago, including Sumatra, Java, Borneo, and the Philippines. As we have seen, it is separated from the Palæarctic region by the Himalayas, continued on the west by a tract of country following the course of the Indus, and on the east by a region curving at first southwards and finally northwards to Shanghai. The south-eastern boundary is an imaginary line, known as *Wallace's line*, which passes between the small islands of Bali and Lombok, then through the Straits of Macassar between Borneo and Celebes, and finally to the east of the Philippines. The islands to the north-west of this line—conveniently distinguished as the *Indo-malayan*

Islands—belong to the Oriental region, those to the south-east—the *Austro-malayan Islands*—to the Australian region. Curiously enough, the zoological differences between the two groups of islands are more marked between Bali and Lombok, separated by a deep channel of only about twenty miles in width, than between Borneo and Celebes, separated by the whole width of the Straits of Macassar.

The most characteristic members of the Oriental fauna are the Orang-utan (*Simia*), the Gibbons (*Hylolates* and *Siamanga*), and numerous Lemurs; the Tiger, which, however, extends into the Palæarctic region, and several Bears and Civets; the Indian Elephant, the Indian Tapir, three Species of Rhinoceros, and the Chevrotains or Mouse-deer (*Tragulidæ*); and several large and handsome Gallinaceous Birds, such as the Peacock, Argus Pheasant, and Jungle-fowl. The resemblances to the Ethiopian Region are numerous and striking, among the most important being the presence of the Elephant, Rhinoceros, the higher Apes, Lemurs, and Manis. On the other hand the presence of Deer and Bears furnish a characteristic difference.

The **Australian Region** includes Australia, Tasmania, and the Austro-malayan islands as defined above, from Celebes and Lombok on the west, to the Solomon Islands on the east, the most important of them being the immense island of Papua or New Guinea. New Zealand and Polynesia are very generally included in this region, but it is more convenient, on the whole, to treat them apart.

The most striking feature of the region is the almost total absence of Eutheria, the Mammalian fauna belonging mainly to the Marsupials and Monotremes. The last-named order is entirely confined to this region, while Marsupials occur elsewhere only in America. The only exceptions are the Dingo or Australian Wild Dog, which is probably indigenous, the universally distributed groups of Rats, Mice, and Bats, and, in some of the islands bordering on the Oriental region, Deer, Civets, and Pigs. The abundance of Marsupials is very remarkable, all the orders of that sub-class, with the exception of the Didelphyidæ, or American Opossums, and *Cænolestes*, being strictly endemic.

Equally striking is the number and peculiarity of the endemic Birds, the most important of which are the Emus and Cassowaries, the Mound-makers or Brush Turkeys (*Talegallus*, etc.), the Birds of Paradise and Bower-birds, the Lyre-bird (*Menura*), the Cockatoos and Brush-tongued Lories. The great number and variety of Parrots, Kingfishers, and Pigeons is also a marked feature, as also is the absence of Pheasants, Woodpeckers, Finches, and other Birds abundant in the Oriental region. Snakes, Lizards, and

Frogs are abundant, and in the rivers of Queensland occur Ceratodus, one of the three existing genera of Dipnoi.

The **New Zealand Region** comprises the three islands of New Zealand (North, South, and Stewart's Islands), together with Norfolk, Lord Howe, and the Kermadec Islands to the north, the Chatham Islands to the east, and the Bounty, Antipodes, Auckland, Campbell, and Macquarrie Islands to the south.

The characteristics of the New Zealand fauna have already been dealt with in some detail. The total absence of land Mammals, with the exception of two Bats and a Rat, the latter probably introduced; the large proportion of endemic Birds, many of which are flightless; the exclusive possession of more than half the known genera, and of a large majority of the species of Ratitæ, and of the entire order Rhynchocephalia; the total absence of Ophidia, Chelonia, and Crocodilia; the paucity of Lacertilia and the almost total absence of Amphibia; all these faunal characters conbine to make New Zealand one of the best marked and most peculiar tracts on the earth's surface.

One or two facts must be mentioned with regard to the smaller islands of the region. In Norfolk Island there existed until recently a flightless Rail, *Notornis alba*, belonging to a genus the only other species of which lives or lived in New Zealand. In Phillip Island, close to Norfolk Island, *Nestor productus* formerly occurred, a member of an endemic New Zealand family of Parrots. In Lord Howe Island there is a species of the endemic New Zealand flightless Rail *Ocydromus*. These three facts all point to a former partial or complete land connection between New Zealand and the islands in question. The remaining islands are closely related to New Zealand, but with greatly impoverished faunæ. In Macquarrie Island, the southernmost land outside the Antarctic circle, there has recently been discovered an Earthworm with distinct South American affinities.

The **Polynesian Region** embraces the numerous groups of islands lying within the tropics to the east and north of the Austro-malayan islands. The most important groups are New Caledonia, the New Hebrides, Fiji, the Friendly Islands, Samoa, the Society Islands, and the Sandwich Islands. They are all typical *oceanic islands*, that is, they are of volcanic origin, have no stratified rocks, and show no indication of former connection with any continental area.

In correspondence with their isolated position, the faunas of these islands, although exhibiting great variety from one group to another, all agree in the absence of land Mammals, except Bats, and—with one or two exceptions—of Amphibia, in the small total number of species, and in the very large proportion of endemic

species. The islands have evidently been peopled by waifs and strays from other lands, at periods so remote that most of the immigrants have assumed the characters of distinct species, or even, especially in the isolated Sandwich Islands, of distinct genera.

On the whole, the affinities of the Polynesian fauna are distinctly Australian; they present, however, certain American characteristics, especially in the occurrence of Lizards, belonging to the American family of the Iguanidæ, in Fiji. Amongst the most notable endemic forms are the Dodo-like Pigeon, *Didunculus*, in Samoa; the Kagu (*Rhinochetus*), a remarkable genus of Grallæ, in New Caledonia, and the *Drepanidæ*, a family of Passerines allied to the American Greenlets, in the Sandwich Islands. Polynesia cannot be said to form a well-defined region, the islands composing it being united largely on the ground of convenience.

In the **Neotropical Region** we have once more an immense tract of land, presenting such well-defined faunal characteristics as make it one of the best-marked of all the zoo-geographical regions. And this in spite of the fact that it is in free connection with the Nearctic regions, the two being separated by an ill-defined transition-region formed by the northern part of Mexico. The Neotropical region includes, therefore, the tropical part of North America, as well as the whole South American Continent, the Antilles or West Indies, the Galapagos Islands, the Falkland Islands, and Juan Fernandez. Both geological and zoological evidence point to a complete separation of the two Americas during the miocene and pliocene periods.

The endemic animals of the region are very numerous and characteristic. They include among Mammalia the Prehensile-tailed Monkeys (*Cebidæ*) and the Marmosets (*Hapalidæ*); the Chinchillas and Cavies, two peculiar families of Rodents; the Jaguar; the Llamas, and Peccaries, and a species of Tapir; the Sloths, Armadillos, and Ant-eaters, three entire families of Edentata. The Opossums (*Didelphyidæ*) are also very characteristic, though not actually endemic since they extend into the Nearctic region. A single Diprotodont Marsupial (*Cænolestes*) has been found in the extreme south. Among Birds the chief endemic forms are the three species of Rhea, constituting the entire order Rheæ; the Tinamous, forming the order Crypturi; the Toucans, Screamers, Oil-bird (*Steatornis*), Hoatzin (*Opisthocomus*), and many others. The Humming-birds, although extending into the Nearctic Region, are a characteristic group. Boas, Rattlesnakes, Iguanas, Crocodiles, and Caimans are abundant, and among the fresh-water Fish are the Electric Eel (*Gymnotus*) and Lepidosiren, one of the three existing genera of Dipnoi.

The negative characteristics of this region are also very remarkable. Except in Central America and the West Indies, there are

no Insectivora; Civets, Oxen, Sheep, Antelopes, and true Swine (*Suinæ*) are altogether absent, and there are very few species of Deer; Crows and Ravens are also practically unrepresented.

In the West Indies there are no Edentata, Monkeys, or Carnivora, and there occurs a peculiar insectivore, *Solenodon*, belonging to the Centetidæ, otherwise found only in Madagascar. The Galapagos Archipelago, a group of Oceanic Islands, about 600 miles to the west of the continent, have at the most two Mammals, a Bat and a Mouse; their Birds are very different from those of the mainland, and include many endemic species; and among the Reptiles are the gigantic Tortoises (*Testudo*), of which different species occur in the various islands.

The general relations of the zoo-geographical regions may be expressed in a diagrammatic form as follows:—

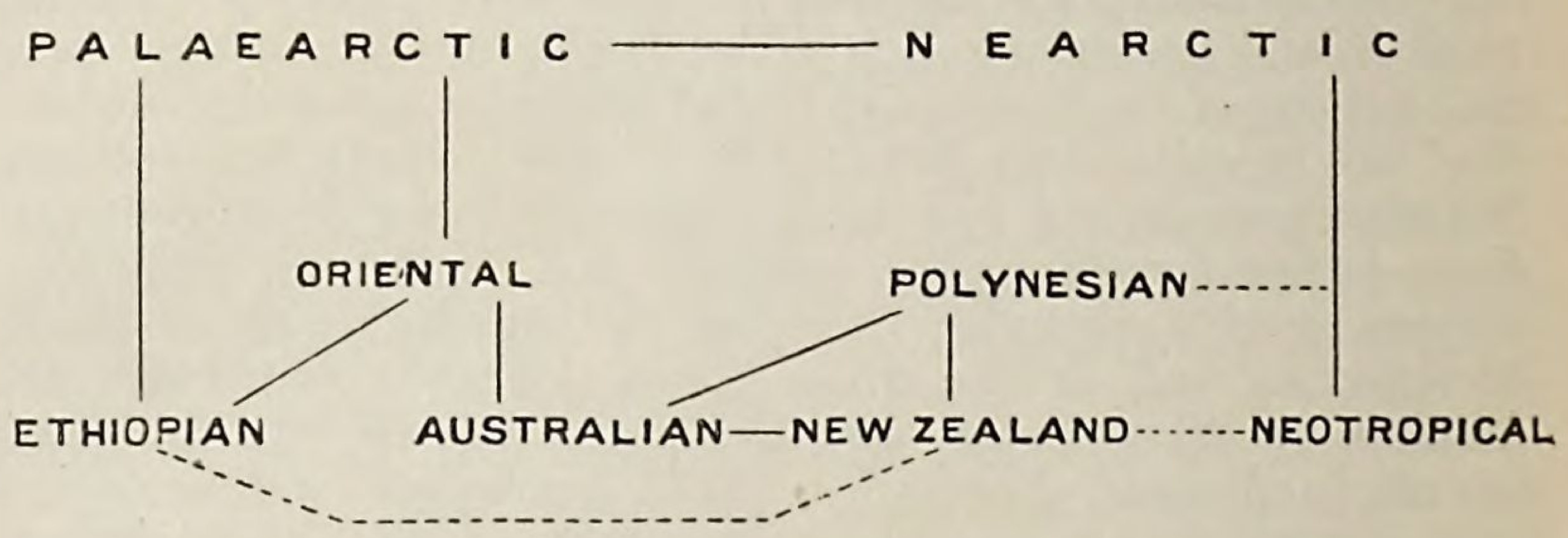


FIG. 1172.—Diagram showing the general relations of the zoo-geographical regions.

2. Bathymetrical Distribution.

The foregoing pages have given a brief sketch of the facts connected with geographical or horizontal distribution. We now turn to bathymetrical or vertical distribution—the facts concerning the distribution of animals at various depths of the sea or of lakes, and at various heights of the land.

The region of greatest abundance of marine life, as regards both the number of genera and species and of individuals, is the **littoral** or **shore region.** The rocks left dry by the retreating tide, the rock-pools exposed at low water, and the forests of kelp at the limit of low tide or a few fathoms below, possess an extraordinarily rich and abundant fauna, including all the Calcareous Sponges and a large proportion of Non-Calcarea, Hydroid Zoophytes, Sea-anemones and Corals, Echinoderms, Turbellaria, Nermertinea, Polychæta, Polyzoa, Brachiopods, decapod Crustacea, Pelecypods, Gastropods, Octopi, and Teleostei. Numerous examples of other groups—Protozoa, the lower Crustacea, Insects, and Elasmo-

branchs—are also littoral, and Penguins, Seals, and Sirenia may be included in the list.

Next in abundance to the littoral is the **pelagic** or **ocean-surface fauna,** including animals which live habitually on the surface or at slight depths of the ocean, often far from land. Amongst them are many Foraminifera, such as Globigerina and Hastigerina, the Radiolaria, the Siphonophora, the majority of Medusæ, both hydrozoan and scyphozoan, the whole class of Ctenophora, many Entomostraca and Schizopods, the hemipterous Insect Halobates, the Pteropoda, Heteropoda, and some other Gastropods, such as Glaucus, most Cephalopods, Pyrosoma and the Salps, numerous Teleosts, such as Herrings, Flying-fish, Mackerel, &c., the greater number of Sharks, and the majority of Cetacea.

The pelagic Invertebrates are mostly distinguished by great transparency, and by being either colourless or of a blue or violet hue. Pelagic Fishes are usually grey or steel-blue above, white beneath, presenting none of the brilliant colours, varied markings, and extraordinary forms so often found among Shore-fishes.

It must be remembered that many littoral animals are pelagic in the larval condition, or during some phase of their life-history, *e.g.*, many Sponges, fixed Hydrozoa and Actinozoa, Echinoderms, Annulata, Mollusca, Crustacea, and Fishes.

The **abyssal** or **deep-sea fauna** is far more abundant than might be supposed from the physical conditions—immense pressure and absence of light and of vegetation. In most parts of the world the bed of the ocean, at depths from 400 to 2,000—2,500 fathoms, is formed of a greyish mud called *globigerina-ooze*, consisting largely of the shells of Foraminifera, such as Globigerina, Orbulina, &c., which have for the most part sunk to the bottom after death. Below 2,500 fathoms the sea-bottom is formed of a red clay, in which shells are absent, having apparently been dissolved during their descent to the greater depth.

Living on the sea-bottom, and most abundant on the globigerina-ooze, are representatives of many groups of animals: Sponges, especially Hexactinellida; a few Medusæ and Corals; examples of all classes of Echinoderms, Stalked Crinoids, and Holothurians being especially abundant; Crustacea, particularly Schizopods and Prawns; and Teleostei. Crabs, Molluscs, and Annulata are rare.

Many abyssal animals are blind, including several of the Crustacea; many others are phosphorescent, and thus supply their own light in an otherwise dark environment. The deep-sea Teleosts are often of very grotesque appearance, with immense heads, wide mouths furnished with long-pointed teeth, extremely distensible stomachs, and phosphorescent organs arranged in rows along the body (see Fig. 834). Other forms, such as the Ribbon

fish (*Regalecus*), attain a great size, and are toothless. When brought to the surface, the expansion of the gases in the interior of the deep-sea Teleosts often bursts the air-bladder, and produces a general disintegration of the tissues.

Plankton, Nekton, and **Benthos**. Besides being arranged with regard to their relations to the shore, the surface of the ocean, and its bed, marine animals are also conveniently classified on the basis of their capacity for movement. Many forms, such as Medusæ, Siphonophora, Ctenophora, Salps, and numerous pelagic larvæ are carried along passively by oceanic currents, their own powers of progression being of the feeblest. Such animals together constitute the *Plankton*, or "drifting-fauna." Others swim actively by means of fins or other appendages, such as the pelagic Teleosts and Elasmobranchs, Schizopods, Prawns, and Squids—they form the *Nekton*, or "swimming-fauna." Others again, have no natatory organs, and are either permanently fixed, like Zoophytes and Stalked Crinoids, or move by creeping over the sea-bottom, like Starfishes, Holothurians, Chætopods, etc.; such forms constitute the *Benthos*, or "bottom-fauna."

The **Fresh-water Fauna** presents certain characteristic features, and is divisible into *fluviatile* forms, inhabiting streams and rivers, and *lacustrine forms*, inhabiting lakes. It is very rich in Lobosa, Heliozoa, Flagellata, and Infusoria, but contains very few Foraminifera and no Radiolaria. Among Sponges there is only a single fresh-water family, the Spongillidæ: among Hydrozoa only four genera, Hydra, Cordylophora, Limnocodium, and Limnocnida, and among Actinozoa and Ctenophora not a single species. There are also no fresh-water Echinoderms or Brachiopods, but many Turbellaria, a few Nemertinea and numerous Nematoda. Among Polyzoa the whole of the Phylactolæmata, and one or two genera of Gynmolæmata, are fresh-water forms; so also are many of the Oligochæta, *e.g.*, Nais and Tubifex, but none of the Polychæta. Fresh-water Entomostraca are numerous and abundant, and belong to all orders except Cirripedia; among Malacostraca there are only some Amphipods and Isopods, the various genera of Fresh-water Crayfishes, and a few Crabs. The larvæ of many Insects are aquatic, and there are several aquatic Spiders. Pelecypods and Gastropods furnish abundant fluviatile and lacustrine forms, although belonging to comparatively few genera; Cephalopods, on the other hand, are wholly absent from fresh-waters, as also are the Tunicata. Among Fishes there are several species of Lampreys, and numerous Teleostei, the Siluroids and Salmonidæ being especially characteristic. There are no fresh-water Elasmobranchs, with the exception of one or two genera of Sting Rays, in the rivers of tropical America, but the Ganoids are a characteristic fresh-water group, although some forms, such as the

Sturgeons, migrate to the sea at certain seasons. The Dipnoi are exclusively fluviatile, and the perennibranchiate Amphibia, as well as the larvæ of the caducibranchiate forms, are characteristic members of the fresh-water fauna. Many Chelonia and Crocodiles; such Birds as Ducks and Grebes; and such Mammals as Otters, the Hippopotamus, and Ornithorhynchus, may also be included in the fresh-water fauna, and some Dolphins are purely fluviatile.

The animal inhabitants of large lakes, like those of the sea, are divisible into littoral, pelagic, and deep-water, and the pelagic forms are, in this case also, characterized by their extreme transparency. Mention must also be made of animals dwelling in deep subterranean caves, shut off from sunlight, such as Proteus, the blind urodele of the caves of Carniola, the blind Fish (*Amblyopsis spelæus*) of the Mammoth caves of Kentucky, numerous Insects, etc. These, like abyssal species, are blind, and usually colourless, and are obviously specialized derivatives of the ordinary fresh-water or land fauna.

In the **Terrestrial Fauna**, also, we find certain groups preponderant, others absent or nearly so. A terrestrial Amœba has been described, and the Mycetozoa are all terrestrial, but no other Protozoa, nor any Sponges, Cœlenterates, or Echinoderms. Among Platyhelminthes we have the numerous species of Land Planarians and the Land Nemertineans, and among Chætopods the whole of the Earthworms. Several Crustacea are more or less completely adapted to terrestrial life, such as the Woodlice, Land-crabs, Cocoa-nut Crab, and Burrowing Crayfish. The Onychophora and Myriapoda are characteristic land animals, so also are most Arachnida and many Insects. Among the Mollusca the only terrestrial forms are the majority of pulmonate Gastropoda. Among Fishes the Climbing Perch, Periophthalmus, and some others are imperfectly adapted to life on land, and the Caducibranch Urodeles, the Anura, and the Gymnophiona are all terrestrial or semi-terrestrial. The Lacertilia, Hatteria, the majority of Snakes, and the Tortoises are land-animals, and so also are many Birds, including all the Ratitæ, the Crypturi, Gallinæ, &c., and the vast majority of Mammals.

Among terrestrial animals, those which habitually live on the open ground must be distinguished from **arboreal forms**, such as Tree-Kangaroos, Sloths, and Monkeys, which pass their lives among the branches of trees, and from **cryptozoic forms**, which live under stones, logs of wood, etc., such as Land Planarians, Peripatus, Centipedes, and Woodlice.

Lastly, we have the **Aerial Fauna**, including animals capable of sustaining themselves for an indefinite period in the air, such

as most Insects, the large majority of Birds, and Bats. The Flying Fishes, Flying Dragons (*Draco*), Flying Phalangers, Flying Squirrels, and Flying Lemur (*Galeopithecus*) are semi-aërial.

The majority of land animals live at or near the sea-level, and as we ascend mountains the fauna undergoes a gradual impoverishment as the snow-line is reached. The higher ranges of all great mountains have a characteristic **Alpine Fauna**. In the European Alps, the Chamois (*Rupicapra*), Alpine Hare (*Lepus variabilis*) and Marmot (*Arctomys marmot*) may be specially mentioned; in the Himalayas, Yaks (*Poephagus*), Musk-deer (*Moschus*), Goats, and Ibexes (*Capra*), besides abundant Birds and Insects; in the Andes, the Condor (*Sarcorhamphus*); in the New Zealand Alps, the rapacious Kea or Mountain Parrot (*Nestor notabilis*).

3. Geological Distribution

In considering the distribution of animals in past time, we are met at the outset with the difficulty that our knowledge of the subject is and must always remain very imperfect and fragmentary. With few exceptions, only calcified, silicified, or strongly chitinized parts are preserved in the fossil state, so that whole classes of animals are absolutely unknown in that condition, and of the rest our whole information depends upon the more or less imperfect skeleton. Moreover, it is only under very favourable circumstances that even the hard parts are preserved; the chances are usually in favour of the animal being devoured or disintegrated before there is time for it to be silted over with mud or sand. And lastly, many rocks have been so altered by the internal heat of the earth as to destroy any organic remains they may once have contained. Thus while palæontology furnishes us with the only sure test of phylogenetic speculation, it is a test which, more often than not, is incapable of application, owing to the extreme imperfection of many parts of the geological record.

It is in the oldest of the stratified rocks that this imperfection is most severely felt. In the **Laurentian** period, forming the base of the sedimentary series (see Vol. I., p. 7), no animal or vegetable remains are known. In certain Canadian serpentine rocks belonging to this period there is found a remarkable structure which, under the microscope, bears a certain resemblance to the supplementary skeleton, with its canal-system, of an immense Foraminifer. On the assumption that it was the fossilized remains of a member of this order, it was called *Eozöon canadense*, but recent researches seem to show conclusively that the supposed fossil is of purely mineral origin. Radiolarians and Foraminifera have been described from the Pre-Cambrian rocks of Brittany, but the nature of the bodies in question has not yet been established beyond dispute.

There are, thus, no undoubted fossil animals until the **Cambrian** period, where many existing groups appear to start suddenly into being. We find Radiolaria, Sponges, Graptolites, Polyzoa, Brachiopoda, Cystoidea, Crinoidea, Asteroidea, Chætopoda (worm-tubes), Phyllocarida, Ostracoda, Trilobites, the generalized Insects known as Palæodictyoptera, iso- and heteromyarian Pelecypoda, Gastropods (Prosobranchs and Pteropods), and tetrabranchiate Cephalopods (Orthoceras, &c.), all, it will be noticed, marine forms, with the exception of Insects.

Proceeding a stage onwards there occur in the **Silurian** period, in addition to the above groups, Foraminifera, Actinozoa (rugose Corals), Ophiuroids, Echinoids, Cirripedes, Scorpions, Eurypterida, Amphineura, Scaphopoda, Elasmobranchs, and Ostracodermi.

Thus, in the two earliest fossiliferous systems are found representatives of all the skeleton-forming phyla, *i.e.*, of all but Platyhelminthes, Nemathelminthes, and Trochelminthes. And, as far as our present knowledge goes, there is no indication of any connecting link between one phylum and another, the primary divisions of the animal kingdom having been apparently as well characterised at that enormously distant epoch as at the present day. Obviously all the older or more generalized animal types which, reasoning from analogy, must have preceded the present well-marked phyla have been destroyed by metamorphic actions or otherwise, without leaving a trace of their existence.

The **Devonian** period is remarkable for its abundant remains of Fishes; Crossopterygii, Chondrostei, and Dipnoi appear for the first time, and all three groups of Ostracodermi are abundant. Decapod Crustacea, of the macrurous or Shrimp-type, also make their appearance. In the **Carboniferous** period, notable for its immense forest flora, there is a great development of air-breathing forms, such as Insects, Arachnids (Spiders), and Myriapoda, as well as Stegocephali, the earliest amphibious Vertebrates. In the **Permian** rocks true air-breathing vertebrates first make their appearance in the form of the reptilian orders, Theromorpha, Sauropterygia, and Rhynchocephalia. This period is also remarkable for the occurrence of Ceratodus, the oldest existing genus of vertebrates.

Thus, by the end of the Palæozoic era, every important class of animals, capable of leaving fossil remains, is represented, with the exception of Mammalia and Birds. Moreover, the Trilobites, the Eurypterida, the Palæodictyoptera, and the Ostracodermi come to an end during this era, no remains of them being known in rocks of secondary age.

Proceeding onwards to the Mesozoic era, the **Triassic** period introduces existing orders of Insects—Orthoptera, Neuroptera, and Coleoptera, as well as Xiphosura, siphoniate Pelecypoda, opistho-

branchiate Gastropods, and dibranchiate Cephalopods (Belemnites). The palæozoic types of Tetrabranchs (*Orthoceras*, etc.) have nearly disappeared, and the Ammonites have become important. Among Vertebrates are found Holostei, Chelonia, Ichthyopterygii, Crocodilia, and Dinosauria, the latter especially being a very prominent group, as well as several Mammalia (*Microlestes*, *Hypsiprymnopsis*, etc.) of uncertain affinities.

In the **Jurassic** period the two highest orders of Insects, Hymenoptera and Lepidoptera, are known for the first time, as well as the reptilian Ornithosauria, and the earliest known Bird (*Archæopteryx*). There are also several small Mammals (*Plagiaulax*, *Amphitherium*, *Phascolotherium*, etc.) belonging either to the Prototheria or to the Metatheria, but occurring in Europe and North America, where there are at present—with the exception of the Opossums—no representatives of either order. This seem to indicate that Mammals originated in the northern hemisphere and spread southwards.

In the **Cretaceous** period the Crab—the most specialized of the higher Crustacea—and the Teleostei—the most specialized of Fishes—make their appearance. Of the last-named group, several Cretaceous genera survive and flourish to the present day, e.g., *Clupea* (Herring), *Esox* (Pike), *Osmerus* (Smelt), and *Beryx*. Ophidia are known for the first time, and Pythonomorpha, Dinosaurs, and Ornithosaurs are important. Mammals are practically unknown, but among Birds the Odontolcæ and the Ichthyornithes are characteristic. By the end of the period five entire groups of Reptiles—the Sauropterygia, Ichthyopterygia, Pythonomorpha, Dinosauria, and Ornithosauria—have become extinct, none of them being known to extend into Tertiary times.

Except in California and Patagonia there is a well-marked break between the Cretaceous and the **Eocene** periods, the fauna of the latter having a comparatively modern character. The Pelecypods and Gastropods belong to existing families and even to existing genera, and Belemnites have almost, and Ammonites quite, disappeared. The Fishes all belong to existing types; Stegocephali have given place to Urodela and Anura, and none of the Reptiles belong to extinct orders. Among Birds, the Penguins, Gulls, Rails, Owls, Picarians (Kingfishers, etc.), and Passeres have appeared, as well as the extinct orders Stereornithes and Gastornithes, and the goose-like Odontopteryx.

But the most noticeable feature of the period is the rise and differentiation of the Mammalia. Among existing orders the Marsupialia (Opossums), Cetacea (*Zeuglodon*), Sirenia (*Eotherium*), Ungulata, Carnivora, Insectivora, Chiroptera, and Primates (Lemurs) appear for the first time, as well as the extinct orders Creodonta, Condylarthra, Amblypoda and Tillodontia, together with the Dinocerata, none of which extend beyond the Eocene period.

In the lower Eocene none of the Mammals belong to existing genera, but in the upper Eocene are found *Didelphys* (Opossum), *Rhinoceros*, *Viverra* (Civet), *Mustela* (Weasel), and possibly *Canis*. The period is also remarkable for the number of annectent or linking forms. There are, for instance, species connecting Dogs with Bears and with Civets, Civets with Hyænas, Hyænas with Cats, Pigs with Pecora, Deer with Chevrotains, Tapirs with Rhinoceroses and with Horses, and so on. It is perfectly clear that the orders, sub-orders, and families of Mammalia, as we now understand them, were, during the Eocene period, becoming gradually differentiated from common ancestral forms.

In the **Miocene** period the Proboscidea (Elephant and Mastodon) make their appearance, as well as a Gibbon (*Hylobates*), and some other Anthropoidea. Many existing families have arisen, such as Hedgehogs, Shrews, and Moles, Mice, Rabbits, and Porcupines; Whales and Dolphins; Tapirs, Hippopotami, Swine, and Antelopes; and species of *Felis* and *Canis*. The Rhinoceroses of the period still have no horns, and the antlers of the Deer are small or absent. The Tapir-like ancestors of the Equidæ found in the Eocene have developed into more Horse-like forms, and the ancestors of the Camels (*Poëbrotherium*) still retain upper incisors and distinct metacarpals. Numerous Diprotodont Marsupials lived in South America during this or the preceding period.

The **Pliocene** fauna has a still more modern aspect, a large proportion of the animals composing it belonging to existing genera, although most of the species are extinct. Complex antlers have appeared in the Deer, horns in the Rhinoceroses, and tusks in the Pigs. The occurrence of Giant Tortoises (*Testudo*) in the pliocene of both Palæarctic and Nearctic regions, and of a Chimpanzee and a true Ostrich (*Struthio*) in deposits of this age in India and the Crimea, indicates the northern origin of these forms. Indeed it seems probable that most of the higher Vertebrata, except Penguins and the New-World Edentates, have originated in the Holarctic region.

In the **Pleistocene** period many existing species have made their appearance, but their geographical distribution is very different from that of the present day. For instance, the European fauna includes many forms now confined to the Ethiopian and Oriental regions, such as Apes, large Felidæ, Hyænas, Tapirs, Rhinoceroses, Hippopotami, Horses, and Elephants, all of which appear to have been driven southward by the cold of the Glacial epoch. In some parts of the world the Pleistocene fauna includes remarkable and often gigantic forms now extinct, the most notable being the great Edentates (*Megatherium*, *Mylodon*, *Glyptodon*, etc.) of South America, the gigantic Marsupials (*Diprotodon*, *Nototherium*) of Australia, and the great flightless Birds (*Dinornis*, *Æpyornis*, etc.) of Madagascar and New Zealand. The occurrence of a Monkey

(*Nesopithecus*) in the pleistocene of Madagascar indicates a closer affinity between that island and Africa than their existing faunæ would indicate.

The Pleistocene passes insensibly into the **Recent** period, which has also witnessed some important zoological changes, especially the extinction of many interesting animal forms, for the most part by human agency. Among these may be particularly noticed Steller's Sea-cow (*Rhytina*), the Great Auk, the Dodo and Solitaire, several flightless Rails (*Aptornis*, *Notornis*, *Aphanapteryx*, etc.), the Phillip Island Parrot, and, above all, the whole great race of Moas.

SECTION XV

THE PHILOSOPHY OF ZOOLOGY

In dealing with the structure and development of the various groups of animals, there has been occasion not infrequently to refer incidentally to various subjects of a general nature, such as evolution, heredity, and the like. Such topics, dealing, not with the concrete facts of the science, but with abstract generalisations deduced from the facts, may be grouped together under the general heading of the philosophy of zoology. The generalisations forming the subject matter of the philosophy of zoology may, in some instances, be so clearly and directly deducible from the data concerned, that it is scarcely possible for any one conversant with the facts to refuse credence to the generalisation. But in other cases the conclusion is a matter of probability only, and one conclusion or another may be regarded as the more probable, according to the estimate formed of the relative importance to be attached to different sets of the facts or to different aspects of the facts. This will become clearer as we proceed; but at the outset it should be distinctly understood that what follows is not to be looked upon in the same light as the statements regarding the known phenomena of animal life which constitute the main substance of the preceding sections. Nearly all the subjects now to be touched upon are, to a greater or less extent, matters in which there may be variety of opinion among those conversant with the phenomena; they are all subjects which will bear discussion from various sides; but, as discussion is here almost out of the question, it is possible to give little more than a brief statement of some of the current views on these questions as an introduction to the study of works specially dealing with them.

The Philosophy of Zoology, or the Philosophy of Biology (for it is here almost impossible to treat Zoology apart from its companion science of Botany), aims at an explanation of the facts of the science. It is observed that an animal possesses a certain

structure, develops in a certain way, has certain affinities with other animals, has a certain geographical and geological range; and the attempt is made to find a satisfactory explanation of these facts.

Evolution.—Of these facts there is, to all intents and purposes, but one explanation requiring consideration here. The animal and plant life of the globe has come to be as it now is by a process of *evolution* which has been going on continuously from an early period in the history of the earth to the present time. The plant and animal worlds, in other words, have been *evolved* by a gradual process of development, in the course of which the higher forms have originated from the lower. Evidence bearing on this doctrine has already been encountered in abundance; in fact the theory of evolution has to be looked upon as in many respects a guiding principle in the study of our science; and it has, accordingly, been necessary in many parts of previous sections to take its truth for granted. In discussing the relations of the various phyla to one another, the relations of the various classes of each phylum, and the position of the type forms within the classes; in referring to the homologies borne by the organs of the members of one class to those of the members of another, it has been necessary to assume the truth of a theory of evolution.

For the evidence, then, in favour of a doctrine of evolution the reader is referred to the substance of previous sections, where it will be found on almost every page. For his guidance some landmarks may, however, be here pointed out.

Anatomical and Embryological Evidence.—A considerable body of the evidence in favour of the view that the higher animals have been derived from lower forms is obtained from the provinces of comparative anatomy and embryology. The mere fact that we are able conveniently to express the resemblances and differences in structure between different groups by the construction of such genealogical trees as have been given in some of the previous sections, tells strongly in favour of a theory of descent; for, though it is by assuming evolution that such diagrams are constructed, the resemblances which they represent point strongly to common ancestry. A theory of evolution explains also the fact that there is running through a whole series of forms—let us say Fishes, Amphibians, Reptiles, Birds, and Mammals—a common type of structure, in which the same essential parts, though perhaps differently modified in accordance with differences in function, are to be found in the same mutual relations. It would be difficult, on any other view of the facts, to explain, for example, the occurrence in the wing of the Bird and of the Bat, the flipper of the Whale, and the fore-foot of the Horse of essentially the same bony elements. More difficult still would it be to explain the cases in which what is a

functionally active and important part in one animal is to be found, though only as a mere vestige, apparently quite useless, in an allied form. Very many instances of this phenomenon will be found in the previous chapters. The wing of the Pigeon is an efficient organ of flight; in the New Zealand Kiwi or Apteryx it is a vestige, not visible externally, being covered over by the feathers, and wholly without function; yet this vestige possesses essentially the same bony framework and the same muscles as the complete and functional wing of the Pigeon. Again, the teeth of the Rabbit are parts essential to the welfare and the very existence of the animal, and persist throughout life, while in the Whalebone Whale teeth are indeed developed in the fœtal condition, but are thrown off before or shortly after birth, never being of any use for mastication or any other purpose. The conclusion that seems to follow from these facts is that it is at least highly probable that the Kiwi has vestiges of wings because it is descended from birds which, like the Pigeon, possessed functionally useful wings; and that the Whalebone Whale has teeth in the fœtal state because it is descended from ancestors which possessed teeth in the adult condition.

The fact that the embryos of animals of one great phylum or class present a great resemblance to one another, and that, the nearer the adult forms are in structure, the closer, usually, is the similarity in their developmental stages, tells strongly in favour of a theory of common descent. Thus the Nauplius stage is found in a considerable number of groups of Crustacea, but it is only between members of families whose structure is closely similar that there is a very near correspondence in the precise character of the Nauplius and in the stages which the larva subsequently passes through.

Evidence of an allied character is afforded by the fact that in the course of its development one of the higher animals sometimes appears to exhibit in successive stages features which are permanent in forms lower in the scale. Thus the embryo of a Mammal presents at an early stage visceral arches and clefts comparable to the branchial arches and clefts of a Fish, and has a blood-circulation in accordance with this; while at a later stage it exhibits in these particulars some resemblance to an Amphibian, later on to a Reptile, and only when development is further advanced takes on its special mammalian characters. Again, we have seen that such an Amphibian as the Frog is, in its early condition as a Tadpole, to all intents and purposes a Fish. Such phenomena may be explained, according to the theory of evolution, by the supposition that the successive stages in the development of the individual animal tend to reproduce, though in a very abbreviated and often greatly modified shape, the stages through which the group to which the animal belongs has passed in the

course of its evolution from lower forms. This supposition—the "biogenetic law," or "recapitulation theory," as it is termed—we shall return to later.

The phenomenon of retrograde metamorphosis observable in many animals, for the most part parasitic in the adult condition, also affords evidence in favour of evolution. It would be difficult to give any other explanation than that afforded by a theory of descent, of the life-history of such animals as Sacculina (Vol. I. p. 553), the parasitic Copepoda (p. 552), or the Ascidians (Vol. II. p. 27). The relatively high organisation of the larva of Sacculina, for example, with its well-marked Crustacean features, can only be explained on the supposition that the shapeless, unsegmented adult has been derived by a process of retrograde development from more normally constructed ancestors.

Most Birds and Mammals, and many animals of lower groups, exhibit a more or less strongly marked sexual dimorphism, the males differing from the females in various other respects besides the character of the sexual organs. Such differences can only be explained by the supposition that they are the result of a gradual process of modification brought about in accordance with the more special adaptation of each sex to its special functions.

Palæontological Evidence.—A second body of evidence in favour of a theory of evolution comes from the side of Palæontology. It might, perhaps, on first considering the subject, be supposed that, had a process of evolution taken place, we ought to be able to find in the rocks belonging to the various geological formations a complete series of animal and plant remains representing all the stages in the evolution of the highest forms from the lowest. Beginning with those strata in which evidence of life first appears, we ought, it might be supposed, to be able to trace upwards, through all the series of fossil-bearing strata, continuous, unbroken lines of descent showing the gradual evolution of all the various forms of plant and animal life. But such a supposition would leave out of account the extreme incompleteness of the history of life on the globe which is preserved to us in the rocks. In the first place, there are many groups of animals and plants which, owing to the absence of any hard supporting parts, are incapable of leaving any recognisable trace of their former existence in the form of fossils. Again, even in the case of such as have such hard parts, the conditions necessary for their preservation in deposits destined to be converted into rock cannot be of very frequent occurrence; and many forms might fail to be preserved simply owing to the non-occurrence of such conditions. In the case of land animals, such as Mammals or Reptiles, for example, when one of them dies, it is for the most part torn to pieces, and even the bones destroyed by various

carnivorous and carrion-feeding creatures. Only now and again would it happen that, by becoming buried in a morass, or swept away by a flood and buried under alluvial deposits, such forms might be preserved.

Again, great thicknesses of sedimentary strata, sometimes containing fossils, can be shown to have become removed by the agencies of *denudation*, or the various forces, such as the action of waves, tides and currents in the sea, of rain and fresh-water streams on the land, by which rock-masses are constantly, where exposed, being worn away; while others, subjected to the pressure of enormous superincumbent masses, and perhaps acted upon by intense heat and other agents of change, have become completely metamorphosed—their mineral constituents having become rearranged, and what organic remains they may have contained completely destroyed. Moreover, of the fossil-bearing rocks that remain unaltered, only a small part can be said to have been thoroughly explored for fossil-remains.

Yet, notwithstanding these causes of imperfection in the record of the succession of life on the earth preserved to us in the rocks, there is sufficient to enable us to judge of the general character of the faunæ (and floræ) of the various geological periods. It is manifest, from what has already been stated throughout the earlier sections with regard to the geological history of each phylum and class, that there has been a general progress in successive eras from the simple to the more complex; the higher forms have, so far as the recorded facts enable us to judge, come into existence later than the lower. The Vertebrata may be taken as an example. There is no evidence of the existence of the highest class—the Mammalia—earlier than the Triassic period of the Mesozoic era. The case of the Birds appears at first sight anomalous; Birds appear for the first time in deposits of Jurassic age, and are therefore more recent than the oldest Mammals. Birds are, however, very highly specialised vertebrates, and, should it be proved that they appeared at a time when primitive Mammals already existed, the separate evolution of the two classes from lower forms would afford a sufficient explanation. Reptiles extend as far back as the Permian. Amphibia, in the shape of the Labyrinthodonts, first appeared in the Devonian; while all the earliest vertebrate remains in the Cambrian and Silurian formations appear to belong to the class of the Fishes. Within each of these classes a progress is usually traceable from older, more generalised types, along diverging lines, to the various specialised forms existing at the present day. In some cases, however,—notably in the Amphibia, Reptilia and Aves,—the orders first represented have become entirely extinct, and have been succeeded by orders that made their appearance on the scene at a comparatively late period.

In certain cases among the Mammalia a number of closely related stages have been discovered, showing, taken in their chronological order, a gradually increasing specialisation of structure. One of the best known examples of this is that of the Horse, to which attention is directed in the section on the Mammalia (p. 572). And there are other families of mammals, chiefly among the Ungulates (the family of the Pigs and various families of Ruminants) in which an equally complete history has been made out.

The direct evidence of the evolution of the Invertebrates is, in general, very imperfect. Some existing types of a comparatively highly-organised character are to be recognised among the fossil remains in the oldest formations—the Cambrian—in which definite organic structures, if we except a few Radiolaria and Foraminifera, are traceable. There is no trace of primitive fossil members of the various invertebrate phyla, and the highly organised air-breathing Arthropods are represented both by Scorpions and by Insects as far back as the Silurian. Such remarkably complete geological histories as have been traced in some of the Mammalia are extremely rare in the Invertebrates. Such direct evidence, however, as is obtainable, points to the probability of evolution, and it may be inferred that the absence of primitive generalised representatives of the invertebrate phyla is most probably due to the imperfect character of the geological record.

The Lamarckian Theory.—Supposing it to be regarded as proved that the organic world has come to be as we find it by a process of gradual evolution, we have next to inquire *by what agencies* this process of development has been brought about.

A sketch of the history of thought on this subject will be given in the section on the history of Zoology, and it will not be necessary here to refer to more than one or two names. The first important attempt to solve the problem regarding the nature of the forces by means of which evolution has taken place, was made, long before evolution was generally accepted among men of science, by Lamarck in his *Philosophie Zoologique*, published in 1809. Lamarck's view was that evolution of new forms has taken, and is taking, place, in great measure owing to the direct action of the conditions of life on the organism, but still more owing to the use and disuse of organs. The surroundings or environment of the animal or plant produce a direct effect on the individual—bring about slight modifications in one direction or another, and these slight differences are transmitted by inheritance to the next generation—such slight modifications going on generation after generation, producing eventually a marked effect on the characters of the organism. The chief agencies that might be supposed to act in this way are climate, the nature of the country, and food. But, in addition to these, Lamarck attributes

considerable influence to the use and disuse of organs. The exercise of a part tends to increase its size and efficiency, and such increase may be and frequently is, according to Lamarck, transmitted to the succeeding generation. In this way, in the course of a number of generations, very great changes might be brought about. To take an example which is often quoted, Lamarck accounts for the great length of the neck of the Giraffe as compared with other Ruminants by the supposition that it has has been brought about by continuous efforts made by the animals through a long series of generations to reach higher and higher among the foliage of the trees from which they derive their main subsistence. Similarly, the disuse of a part, in Lamarck's veiw, gradually leads to its diminution, and perhaps ultimately to its complete disappearance. In this way he would explain the disappearance of the hind-limbs in the Cetacea, of both pairs of limbs in the Snakes, of the olfactory nerves in aquatic Mammals, and so on. Whether differences which are produced in the individual organism by surrounding conditions or by its own efforts are transmitted by inheritance to succeeding generations is not yet a settled point: we shall have again to refer to this question —the question of the *inheritance of acquired characters*—at a later stage. That such inheritance, if it takes place, could account for the development of all the various groups of animals and plants is not held by many biologists at the present time.

Darwinian Theory.—It is to Charles Darwin that we owe the most thorough and consistent explanation of evolution that has hitherto been put forward—the explanation known as the theory of Natural Selection. The development of this theory and the share taken in it by Wallace will be sketched in the historical section. The two main supports of this theory are two sets of biological phenomena known respectively as the *struggle for existence* and *variation*, both of which have to be understood before it is possible to grasp the theory of natural selection.

Struggle for Existence.—In order that it may flourish there are necessary for every species of plant and animal certain conditions. The plant must find a place with soil containing certain constituents, a certain degree of moisture and of sunlight. For spots presenting the necessary favourable conditions there is constantly going on a competition between individual plants of one species and between the members of different species. The nature of this struggle is well seen when a piece of garden ground is allowed to run to waste. Its surface is soon overgrown by weeds of a variety of kinds, which kill out some of the original garden plants. Byandby the more hardy weeds kill out and replace such weaker forms as may first have obtained a footing, till an entirely new set of weeds may take the place of those that first appeared. Again, it was shown by Darwin that in turf which

is kept cut close a much greater number of plants are enabled to grow than is the case if the turf is allowed to grow freely. If the turf is not kept cut some of the stronger plants gain predominance and kill out weaker forms. In a space of turf on which Darwin experimented, no less than half of the species present in the turf when kept pretty closely shaven perished when it was allowed to grow freely.

Plants, however, have not only to compete with one another for space and light and nourishment. They have also numerous animal foes to contend with. A large proportion of young seedling plants are destroyed by various insects and by snails and slugs. One of Darwin's experiments bearing on this point was to clear and dig up a small plot of ground and watch the fate of the seedling plants that sprang up on it: he found as a result that some four-fifths were destroyed by insects, snails, and slugs. But it is not the lower forms of animals alone that are thus destructive to plants. Many of the Mammalia, particularly, as we should expect, the herbivorous Ungulata, exercise a strong influence in this way. Cattle, and Goats particularly, sometimes produce a marked effect on the flora of a country. The introduction of Goats has been observed gradually to destroy the forests of certain districts—the seedling plants being eaten as they appear, and thus no young trees being developed to take the place of those dying from old age or other causes. The mere enclosing of a piece of moorland by means of a fence was observed by Darwin to have resulted in the growth of a number of trees. In the unenclosed parts the young trees were never able to make any headway against the cattle by which they were constantly being browsed down.

Among animals, with which we are here more particularly concerned, as well as among plants, a struggle for existence goes on on all sides. To begin with, before there is any struggle for existence in the strict sense, there is—particularly in lower groups—a very great indiscriminate destruction of ova and young embryos. Most lower animals produce ova in great number, hundreds, more often thousands and tens of thousands, annually. Only a few of these reach maturity; a large proportion are destroyed indiscriminately at one stage or another of their development, some failing to reach a spot favourable for their development, others becoming the food of other animals. But such of the young as are less adapted to escape the various dangers to be encountered, and less fitted to procure the necessary food, are more likely to be destroyed. This is one phase—and the most important, perhaps, of all—of the struggle for existence among animals. But there is also a struggle for existence, not only between individual animals of the same kind, but between animals of different kinds. This struggle, in so far as it relates to the competition for food and shelter, is more

severe between nearly-related species; for in such a case the food and the favourable conditions required are the same or nearly so in the two competitors. But there is also a struggle for existence of a constant and severe kind which goes on between carnivorous animals and the animals on which they prey—a struggle in which the defensive qualities of the latter, such as swiftness, power of eluding observation, power of resisting attack and the like, are opposed to the predatory powers of the former.

Variation.—It was by observing this struggle for existence constantly going on in nature, taken in connection with the phenomenon of *variation*, that Darwin was led to his principle of natural selection as accounting for evolution. Variations in domestic animals and cultivated plants are observed to take place in all directions. Taking advantage of this, man has been able to select, in the animals which he has domesticated, and the plants which he has cultivated, those qualities which seemed most likely to be useful to him; he has thus been able to produce, from one and the same original wild stock, widely different varieties specially adapted for different purposes. Thus from one wild species of plant of the order *Cruciferæ*—viz., *Brassica oleracea*—have apparently been produced all the varieties of cabbage, cauliflower, broccoli, Brussels sprouts, and other forms, each with a peculiar and strongly-marked growth of its own. All the domestic vegetables afford us instances of the same thing, and so do all the cultivated fruits. The crab-apple or wild apple, for example, was the original of all the varieties of apple, amounting to about a thousand, cultivated at the present day—varieties presenting in many cases very great differences in size, colour, texture, flavour, time of ripening, and other qualities. In cultivated flowers, the same holds good in an even higher degree.

The instances of variation observable among domestic animals are still more striking. The domestic Dog, for example, exhibits a large number of very marked varieties. Though all these seem to be fertile with one another, and to produce fertile offspring, it is generally supposed that they have been derived from several wild species with more or less hybridisation. But the enormous differences which are to be observed between some of the varieties have been produced to a great extent under domestication. These are not all mere superficial differences, but involve also the proportions and shape of the parts of the skeleton. The difference in the form of the skull and in the proportions of the bones of the limbs between a Greyhound and a Bulldog, for example, are very remarkable—so great, in fact, that if they were found to occur between two wild forms they would justify a zoologist in referring the two to distinct genera. Sheep and Cattle, Pigs and Horses present similar, though not perhaps quite so strongly-marked, varieties. One of the most remarkable cases of variation under

domestication, and one to which Darwin paid a good deal of attention, is that of the domestic Pigeon. Of this, there are a considerable number of varieties, known to fanciers as pouters, fantails, carriers, tumblers, and so on; and it appears to be almost certain that these are descended from one wild species—the blue Rock-pigeon.

These varieties, and many more that might be mentioned, have been produced by man *selecting* those forms that tended to vary in a desired direction—have been produced, that is to say, by *artificial selection*, sometimes consciously exercised, sometimes, no doubt, unconsciously. This process has had a long period of time for its operation, many of our domestic animals and plants having been the objects of care and cultivation in Egypt and Western Asia certainly several thousand years ago; in many cases the wild forms from which they were developed appear to have become totally extinct.

But variation occurs among animals and plants not only under domestication; it occurs also in a state of nature. Evidence of this has already been adduced in the account of certain of the examples of the various phyla; and in the examination of specimens of these in the laboratory the student can hardly have failed to notice the occurrence of *individual differences* not due to differences in sex or age in animals of all classes. In this respect, in the strength of the tendency to individual variation, there is a very great inequality between different species of animals, some being extremely variable, some comparatively stable. Variations of external parts have naturally, from the greater ease with which they may be observed, attracted most attention, but the examination of the internal parts in large numbers of individuals of the same species, when it has been carried out, has shown that variations in internal organs are also of great frequency.

Among the Protozoa, the Foraminifera are characterised by numerous and marked variations—so marked as "to include, not merely those differential characters which have usually been accounted *specific*, but also those upon which the greater part of the *genera* of this group have been founded, and even, in some instances, those of its *orders*." The Mollusca vary also very frequently and extensively, especially in the form and markings of the shell; and of some of the species which have been most completely studied in this respect a very large number of more or less strongly marked varieties have been recorded. Many of the Crustacea are also extremely variable in coloration and in the length and proportions of the various appendages. But, among the Arthropoda, it is in the Insecta, and more especially the Lepidoptera, that we find the most striking instances of variation. In the Vertebrata, also, variations in colour and proportions, as well as in internal organs, occur frequently in all classes.

Natural Selection.—According to Darwin's theory of *Natural Selection*, nature, *i.e.*, the conditions under which the organism exists, selects certain variations as they arise, very much as the breeder or the gardener selects variations in domestic animals or cultivated plants. Let us see how this selection is carried on. We have seen that there is going on, on all sides, a struggle for existence. It is at first difficult to realise the intensity of this struggle, for there is little appearance of it on the surface. If we consider, however, that a large proportion of living things prey on living things of other groups, and when we bear in mind the extremely small proportion which, in most cases, the surviving individuals of any group bear to the number of young produced, we come to understand that this struggle for existence must be general and intense.

Now in the case of a species living under tolerably uniform and stable conditions as regards climate, food-supply, and the like, the effects of this struggle would be the *survival of the fittest*. Of the young produced only a small proportion (in most cases) reach maturity; some of these surviving forms have survived, perhaps, because they have happened to escape being preyed upon by enemies, while others have succumbed; but there can be little doubt that, in the long run, such individuals will survive as are best fitted to cope with the conditions to which they are subjected —such as are swiftest, let us say, in escaping pursuit; or such as, by their special shade of colour or the nature of their markings, elude the observation of an enemy; or such as, by reason of their thicker covering, can better endure extremes of cold. Such surviving individuals would, it is assumed, transmit their special properties to their progeny, and there would thus be a gradual approximation towards a better adaptation of the species to its surrounding conditions by virtue of this "survival of the fittest."

Let us suppose the conditions to change. Gradual changes in climate and other conditions are known to take place owing to subsidence or elevation of the land. But conditions might be changed in many other ways: some animal or plant previously used as food might become exterminated; or a new enemy might find its way into the district inhabited by the species. Then such individuals as presented variations which enabled them better to cope with the new surroundings would have the advantage over the others, and would have a much better chance of surviving, and leaving progeny. The useful variations thus produced and transmitted to the progeny would tend to increase, generation after generation, until a form sufficiently distinct to be regarded as a new species had become developed from the original one.

The process of survival of the fittest has a reverse side, which has been termed the *elimination of the unfit*. Of the varieties that appear some are less completely adapted to their surroundings

than the majority, and these (the conditions remaining the same) tend to become destroyed owing to their unfitness to cope with their environment. The result of this process of elimination (apart altogether from the selection of progressive variations by which evolution, according to the theory, proceeds) is to keep up a certain standard of efficiency in the organs of the members of the species. Under certain conditions this *sustaining* influence, as we may term it, of natural selection may be suspended; the organism may be placed under conditions in which natural selection acts with reduced effect or does not act at all. There is, under such circumstances, no "elimination of the unfit"; and, as a result, fit and unfit survive indiscriminately, inter-breed, and produce offspring, the ultimate outcome in the course of generations being a gradual deterioration in the whole race.

This suspension of the influence of natural selection, with its results, has been termed *cessation of selection*, or *panmixia*. Panmixia acts more commonly on single organs than on the entire organism. Thus, if, owing to some change in surrounding conditions, an organ is no longer useful, it is no longer kept up to the previous degree of efficiency by the elimination of the individuals in which the organ in question is imperfectly developed, and, as these cross with one another, offspring is produced in which the organ is below the efficient standard; and by a continuance of this process through a series of generations, it is supposed that the organ gradually dwindles in size, and may altogether disappear. Thus at that stage in the ancestral history of the Cetacea in which they had come to adopt a purely aquatic mode of life and no longer visited the shore, the hind-limbs, being no longer of service, would no longer be maintained by natural selection, and would gradually decrease in size until, finally, they entirely disappeared. In the case of these, as of many other rudimentary organs, however, it is probable that natural selection played a *positive* part in bringing about their diminution. Under the conditions supposed, the possession of hind-limbs would probably be an actual disadvantage to the animal, acting as an impediment to the swift progression through the water, and interfering with the free movements of the tail; and varieties with diminished hind-limbs would, therefore, possess an advantage over their fellows in the struggle for existence. There would then be a positive *reversal of selection*.

A special phase of Natural Selection is distinguished under the title of **Sexual Selection.** By means of Sexual Selection it is attempted to explain the greater part of the secondary differences between the sexes which are so striking in many groups of animals. The special part which each sex has to play in the fertilising and deposition of the ova, in protecting and procuring food for the young, requires qualities, both anatomical and psychical, of a more

or less widely divergent character in the male and female. Between the males of animals of many groups, contests frequently take place, and this affords us an explanation of the presence or special development in many cases in that sex of various offensive and defensive weapons—horns, tusks, and the like. Similarly, we are able to understand the greater vigour, in the majority of cases, of the male, with concomitant greater intensity of coloration, and the development of various ornaments and excrescences not present in the female. In many groups of Insects, and in a large proportion of Birds, sexual differences in coloration are very marked. These are, in some instances, to be traced to the necessity for different protective resemblances required in the two sexes owing to different habits, or to the necessity for protective colorations and markings in the female and not in the male. In the case of Birds, when the sexes differ, as they do in a large proportion of the species, the male has always more brilliant coloration, and often possesses also special crests or frills, wattles and the like, not present or less developed in the female. The greater obscurity of the colouring of the female Bird appears to be adapted to rendering her less conspicuous to enemies, such as Birds of Prey, while sitting on the nest; and, in cases where the females are brightly coloured, the nest is covered over above, or is constructed in a hole in the ground. The brilliant colouring and other features distinguishing the males of many Birds may be in great part the by-product of higher vitality, and may thus be the indirect outcome of natural selection leading to the more vigorous males obtaining an advantage in contest with rivals. It is possible, also, that the choice of the female in selecting a mate may have been a factor in bringing about the special modifications in question. But the evidence which has been adduced for any such selection on the part of the female of a mate with some slight superiority in brilliancy of colouring, or the development of crests and the like, over his rivals, is insufficient, and many observations tend to show that selection of this kind, though it may occur, is exceptional.

Protective and aggressive Resemblance and Mimicry.—One of the most important of the phenomena which are well explained by the theory of natural selection and which may, therefore, well be taken as affording evidence in favour of that theory, are the phenomena of *protective resemblance*, *warning characters* and of *mimicry*. In innumerable cases among all classes of animals there are found instances of a resemblance between the animal and its ordinary natural surroundings, which has the effect of rendering it inconspicuous and unlikely to attract the observation of an enemy, or of its prey. Such a resemblance is brought about sometimes merely by colour, very often by the arrangement of the colour in a pattern, this being frequently accompanied by modifications of shape

including sometimes the development of special excrescences or appendages. In some cases of protective resemblance the colour, and even the markings, change with a change of the surroundings. For details of such cases reference must be made to special works. Many Insects present elaborate markings which give them a close resemblance to a tuft of lichen or moss, a twig, a leaf, or other object, and resemblances of an equally striking character occur in other classes.

Some animals, more especially certain Insects, are protected by their nauseous character against being devoured by aninals that would otherwise prey upon them; but often, no doubt, such nauseous Insects are attacked and killed before their unpalatable character is detected. It is thus manifestly of advantage to such animals that they should be readily recognisable, and should thus be passed over: and in many such cases the coloration is bright and conspicuous, or the animal is rendered conspicuous by other means (*warning characters*).

By *mimicry* is meant a superficial resemblance borne by one animal to a member of a different group. The best-known examples of mimicry occur among the Insects. It is manifestly of advantage to a Butterfly belonging to a group which is not nauseous to be readily mistaken for a nauseous form with conspicuous warning colours and markings, and this appears to be the explanation of many cases of mimicry. Similarly, a variety of flower-frequenting Dipterous Insects which have no sting or other weapon, bear a remarkable resemblance to Bees or Wasps, belonging to a distinct order (the Hymenoptera)—the resemblances embracing, not only shape, colour, and markings, and development of hairs on certain parts, but the movements of the wings and other parts and the humming sounds emitted, so that, on a superficial inspection, the mimicry appears complete.

Heredity.—The various characteristics of a plant or animal are transmitted, with or without modifications, to the succeeding generation.

In the highest groups of animals this transmission is effected only through the intermediation of the sexual cells—ova and sperms—since they alone are capable of giving rise to a new generation. But in lower organisms the faculty of reproduction is more widely diffused among the component parts; in some lower multicellular plants each and every cell is capable of taking on the function of reproduction and giving rise to progeny similar in all respects to the parent; in other words, every cell in such cases must contain germinal substance. In other, somewhat higher, forms the germinal substance, though still widely diffused, may not be present, or capable of becoming active, in all parts, and may be confined to the cells of one or other of the layers. In the vegetable kingdom, even amongst the highest forms, the germinal

substance can be shown to be widely diffused throughout the plant. Thus in many flowering plants, if we cut a shoot into lengths the pieces are all capable of giving rise under suitable treatment to complete plants with flowers containing reproductive cells, and in many cases a leaf, or a portion of one, is capable of a similar development. In many animals a similar wide distribution may be shown to prevail. This appears most strikingly in forms that multiply by budding. In Hydra, for example, any part of the body seems capable of giving off buds, and in the buds, after they have become separate, ova and sperms are developed from the cells of the ectoderm. A similar phenomenon is to be observed in other Cœlenterates and in the Polyzoa and the Composite Ascidians, and also in certain cases among the Platyhelminthes and Annulata. In all these, and other cases that might be mentioned, the germinal substance is not confined to the reproductive cells, new reproductive cells being capable of being formed from the substance of the cells of various tissue-layers.

The phenomena of *regeneration* are important in connection with this question of the site of the germinal substances. Many members, not only of the lowest pyla, but of the Echinodermata, the Annulata, the Arthropoda, the Mollusca and the Chordata, are able, as has been repeatedly mentioned, to replace, by a process resembling budding, parts that have been broken off: some of the cells of the adult body must, therefore, in these cases retain in a certain degree the faculty of reproduction, and must contain germinal substance. The germinal substance concerned in regeneration, must, it is of importance to note, be capable of being stimulated into activity in a certain definite direction by an influence brought to bear upon it from without.

In the Vertebrata the power of regeneration, if we leave out of account the various epidermal structures, is exceptional, and where it occurs (most Amphibia, some Reptiles) it is confined to the limbs or the tail. In the highest Vertebrates there is no power of regenerating a lost limb or tail, and the capacity for reproduction is confined to the sexual cells.

A remarkable *persistency* characterises these reproductive cells. By their means there are handed down from one generation to another, with little alteration, all the characteristics of the species of plant or animal. This special faculty of the reproductive cells is the faculty of *heredity*.

Heredity does not imply absolute fixedness of all the characteristics inherited by one generation from its predecessor. On the contrary, as already pointed out, variations are constantly presenting themselves. Some of the variations which animals exhibit are a direct result of the action of surrounding conditions, or of the use or disuse of parts, on the fully developed animal; we can in some cases actually cause the animal to change to a more

or less marked extent by placing it under different conditions. Another set of variations produced by the action of external influences on the organism only appears if the action takes place in the course of development at one stage or another between the oosperm and the adult. Of the occurrence of both these forms of variation we have direct and positive evidence. It is a familiar fact that increased exercise of a part tends to an increase in the bulk of its muscles. The colours and markings of certain Fishes can be altered at will (of course within certain limits) by changing the material on the bottom of the aquarium in which they are confined; the colours of many Caterpillars may be altered by changing the colour of their surroundings. A third set of variations probably also occur, though direct evidence is wanting, namely, variations which may arise within the sexual cells before the union of ovum and sperm, or which may result from that union. The former two sets of variations are generally spoken of as "acquired characters"—new characters acquired during the lifetime of the individual—but their nature would be more clearly indicated by terming them *extrinsic* variations, as contrasted with the *intrinsic* variations forming the last group.

The extrinsic variations being brought about by the action of external conditions, their causes are very various. In every such case the organism responds to some persistent external influence by undergoing some more or less persistent change. Mutilations, the rapid mechanical removal or destruction of parts, are here, by the terms of the above definition, excluded from the class of variations altogether, since, though the change involved is frequently permanent, it is effected by an influence which is temporary in its character. This, as will be seen, is of importance in connection with the next question we have to deal with—the inheritance of acquired characters.

Can acquired characters or extrinsic variations be transmitted by inheritance? That they can be is of the essence of Lamarck's doctrine of development, which, in fact, may be described as a theory of development by means of the inheritance of extrinsic variations or, as it is sometimes called, *use-inheritance*. But the maintenance of the view that extrinsic variations may be transmitted is not inconsistent with the acceptance of natural selection as a true cause of evolution. Evolution might be supposed to be due to the selection and inheritance of both intrinsic and extrinsic variations. From the nature of the case, evidence in favour of the inheritance of extrinsic variations on the one hand, and the occurrence of intrinsic on the other, is extremely difficult to obtain. One or the other must occur, or there would be no evolution. But to prove in any given case that a change is due to the one factor rather than to the other, is extremely difficult. When a character not present in the parents

appears in the offspring, there is, to begin with, great difficulty in proving that it is really new: characters not present in the parents are known to be frequently inherited from a more or less remote ancestor. But, if we suppose it to be established that the character is a new one (and absolutely new characters must appear, or we should have no evolution), then it would require a very accurate knowledge of all the circumstances to enable us to be certain whether the appearance of the character is not due to the action of some external influence on the parent, either during development or in the adult state, rather than to a change arising within the reproductive cells. Instances are frequently brought forward which have been supposed to afford evidence of the transmission of mutilations from parent to offspring; but such a transmission must, from the nature of the case, always be extremely difficult to prove, and the majority, at least, of such cases are found, on a careful analysis, to be capable of other interpretations. On the other hand, though well-established cases of the inheritance of mutilations would greatly support the doctrine that acquired characters are transmissible, the negative results that have attended certain experiments on mutilation are of little value in the direction of proving that extrinsic variations *cannot* be transmitted, since, as has already been pointed out, such experiments in mutilation cannot be said to reproduce the conditions under which an extrinsic variation might be supposed to be transmitted; the mutilation is instantaneous; the variation must be supposed to be the result of long-continued action, which, it might be expected, would have a sufficiently profound effect to engraft it permanently on the organism.

It should be pointed out here that there is no absolutely hard and fast line to be drawn between the intrinsic and extrinsic variations, since changes in the sexual cells may very well be due, directly or indirectly, to influences exerted from without. The material from which reproductive cells may subsequently be fashioned is, in plants and in many animals, in such close and intimate union—so far as can be seen—with the other protoplasmic elements of the organism, that it seems highly probable that influences affecting the latter may in many cases affect also the former.

Another question that presents itself in connection with heredity is, Can any special part of the germ-cell be fixed upon as the part specially concerned in hereditary transmission? Certain experiments which have been made on the ova and sperms of Sea-urchins have an important bearing on this question. It has been found that an ovum artificially deprived of its nucleus will develop if a sperm (consisting mainly of nuclear matter) be introduced into it to take the place of the original nucleus. And, further, it has been shown that if an ovum of one species be

deprived of its nucleus, and a sperm of another species be introduced, the ovum develops into an embryo which has the special peculiarities of the embryo of the second species, and not of that of the first; it being thus proved that the cytoplasm of the ovum is not active in the transmission of special characters, while the sperm is. In this case the transmission of the special characters of the second species must obviously be due to the sperm; and since the cytoplasm of the ovum seems to be inactive in this direction, it is likely that the same is true of the cytoplasm of the sperm, and thus the conclusion is arrived at that it is nucleus, and not cytoplasm, through which the transmission of specific characters takes place. But during ordinary impregnation it has been shown that the penetration of the sperm into the ovum involves the entry, not only of a nucleus (the male pronucleus), but of a centrosome; and it is quite possible that the latter may take a share in transmission. If, as appears probable, the nucleus is the chief vehicle in this process, the chromatin loops are the parts of the nucleus which, on account of their regularity of form and the regular nature of the changes which they undergo during cell-division, are usually set down as containing the germinal matter. Accordingly, certain theories of an ideal character, which there is not space to touch upon here, have been put forward, aiming at enabling us to picture to ourselves the way in which the hereditable characters are stored up, combined, and transmitted. It is well to bear in mind, however, that there are other structures in the nucleus besides the chromatin loops—structures which, though less conspicuous optically, may have as much to do with transmission as the chromatin.

Though the experiment referred to above, of substituting a sperm of one species for the nucleus of an ovum of another, and obtaining as a result the development of a larva with the special characters of the larva of the former species, shows that the nucleus of the sperm bears some of the more superficial features by which one species is distinguished from another, it by no means proves that the cytoplasm of the ovum does not bear many of the more general characters; the cytoplasm of the ovum of an Echinus may be the bearer of the more fundamental characters by which an Echinid differs from other Echinoderms and by which Echinoderms differ from members of other phyla. In short, so far as these experiments go, the cytoplasm of the oosperm may be the bearer of all the more ancient features—the nucleus only of those which are more recently acquired.

It has been urged in connection with the question of heredity, that what is transmitted from generation to generation is not so much matter as energy. The quantity of matter is always relatively small; the important fact appears to be that this

relatively small particle carries with it potential energy sufficient to effect the structural changes which precede the beginning of the process of assimilation, and to at least initiate that process. But we can hardly imagine a succession of complicated and very definite changes of structure, such as are involved in the development of an animal, taking place unless the germinal matter in which they originate has a correspondingly complicated and definite structure.

The oosperm, having the faculty of reproducing the entire animal without (in many cases) any further influence emanating from the parent, must contain within itself something to represent each of the parts—even each group of cells—of the adult body. The oosperm of a Frog, for example (p. 267), simple though its structure appears to be, must contain potentially within itself all the characteristics of the adult animal, and not only those, but the characteristics of each successive stage in the formation of the tadpole and its metamorphosis into the adult Frog. Attempts have been made to explain how it is that the reproductive cells acquire this reproductive capacity. One of the most interesting of these is a theory which is termed *pangenesis*, the origination of which is due to Darwin. According to this theory, the cells of the various parts of the body throw off minute ultra-microscopic particles or "gemmules," and these find their way by various channels to the developing reproductive cells, in which they accumulate until each reproductive cell contains gemmules representing all parts of the body. When development takes place each gemmule develops into the part corresponding to that from which it has been derived.

If this theory afforded a true explanation of the facts of reproduction, there would necessarily be accumulated in the ovum gemmules representing, not only every part of the body of the adult, but also every stage in the development of the embryo, and (since we see ancient ancestral characters occasionally reverted to) something to present the special peculiarities of former generations. Now it is a question if such an accumulation of gemmules, each necessarily several times the size of a chemical molecule, would not form a mass very much larger than an ovum. Such a doctrine would, moreover, hardly appear to be necessary in order to explain the facts. The accumulation in the ovum of the hereditary tendencies (as we may call them) may only in part take place during the life-time of the individual: a good part of them—all, perhaps, except such as have been more recently acquired—might be contained in the ready-formed germinal material handed down from previous generations.

Against a hypothesis of pangenesis such as was formulated by Darwin, the mode of reproduction of many plants tells more strongly perhaps than any of the facts derived from the animal

kingdom. Many of the higher flowering plants, for example, are capable of being propagated by means of a cutting of the stem or root, or even by a leaf. As the new plant developed from the cutting gives rise to flower and fruit, the cutting must contain germinal matter; and germinal matter, must, therefore, be diffused throughout the cells of such a plant. Pangenesis, unmodified, would require that in such a case a large proportion of the ordinary cells of the plant should receive gemmules derived from all parts.

It is a moot point whether it is possible that any influence (such as is pre-supposed in pangenesis) can pass from the cells of the various parts of the body to the ova—whether there can be any communication of substance carrying with it tendencies to be transmitted to the next generation. It is certain, however, that an influence of a *centrifugal* character is exerted by the sexual cells. The absence of ovaries or testes has, in many cases, a marked effect on certain of the characters—an effect on the development and form of certain of the parts. This is seen not only in higher animals (Mammals and Birds), but also among some lower forms. In certain crabs, for example, the presence of Sacculina, a parasitic rhizocephalan nourished at the expense of the testes, which become destroyed, produces a very marked alteration in some of the external features. But, while this is the case, an influence exerted in the opposite direction—an influence transmitted from the other parts to the germ cells, has not been proved, and from the nature of the case perhaps cannot be directly proved. Such an influence, it is hardly necessary to add, must be pre-supposed if we assent to the doctrine of the inheritance of acquired characters.

It has been already mentioned (Vol. I., p. 18) that the ovum, before developing, undergoes a change termed *maturation*, consisting in the separating from it of certain relatively small portions of its substance, which are known as the *polar globules*. A connection between this process and the phenomena of heredity has long been supposed to exist, and a variety of theories have been put forward aiming at an elucidation of this. It has been supposed that, in order to fit it for the reception of the sperm, the ovum had to get rid of a certain part of its substance—the ovum, regarded as a hermaphrodite cell, had to become female by the discharge of the polar globules representing the male part of the hermaphrodite cell, before it was adapted to form the oosperm. This view appeared to be supported by the supposed absence of polar globules in the case of parthenogenetic ova, since in such instances, no male element being added, the ovum would be the equivalent of the oosperm without undergoing any change. But polar globules are now known to occur in at least some parthenogenetic ova. Other theories of maturation have been elaborated, but in

considering this question perhaps the most important point to attend to is that the process is one of cell-division (with its attendant changes in the nucleus) and that the result of it is the formation of three or four cells, one—the ovum—very much larger than the rest. The polar globules may thus very well be regarded as abortive ova. This, however, is not in itself a sufficient explanation of their occurrence in all classes of the Metazoa from the lowest to the highest. Mere vestiges are hardly likely to be so persistent; so that we should be justified in concluding that the polar globules are abortive ova which persist in all classes of animals because of some function that they perform in preparation for development—probably in removing material no longer required, or calculated to retard impregnation and development.

If, as is admitted by many writers at the present day, natural selection—the selection of intrinsic variations—be inadequate to explain many of the facts of evolution, there is no alternative but the view that development is partly caused by the transmission of changes brought about in the organism as a result of its own activity, directed and conditioned by the environment, and of the action of external agencies. By what means such changes can become impressed on the germinal substance it is difficult to understand. But, as already pointed out, a centrifugal influence of the reproductive cells on the development of distant parts is established by numerous instances, and the mode of transmission of the influence is as difficult to conceive in the one case as in the other.

SECTION XVI

THE HISTORY OF ZOOLOGY

ZOOLOGY, like other branches of Natural Science, has had two lines of progress, observation and generalisation. Without accurate and detailed knowledge of the facts and phenomena of animal life and structure, all theories of classification or of origin are so much idle speculation: in the absence of the philosophic spirit suggesting hypotheses of greater or less magnitude, the mere accumulation of facts is an empirical and barren study.

Zoology as a science, therefore, can hardly be said to have existed until a sufficient proportion of the facts relating to animals had been observed and recorded accurately and systematically, and until some attempt had been made to classify these facts and to arrange animals into larger and smaller groups according to some definite plan.

This being the case, it may be said that the common knowledge of animals possessed by mankind in all ages, and constantly being developed and extended by lovers of external nature and by anatomists working from the medical standpoint, first became scientific and evolved itself into a system some 200 years ago, when **John Ray,** an English non-juring clergyman, first grasped the idea of species and published the earliest classification of animals founded upon anatomical characters. Although soon overshadowed by the greater genius of Linnæus, Ray may safely be called the father of modern zoological science, the only serious precursor of his *Synopsis methcdica animalium*, published in 1693, being the voluminous *De differentiis animalium* of **Edward Wotton,** printed nearly 150 years earlier.

But although Zoology, as a science, was practically non-existent up to the period referred to, much valuable knowledge of animals had been accumulated, and was, as it were, merely waiting to be systematised. As in other branches of knowledge, the first steps were taken by the Greeks, and, in philosophical grasp, the

zoological writings of **Aristotle** (384–322 B.C.) are far in advance of those of all other students of the subject up to the times of Wotton and Ray. His treatises, especially *The History of Animals*, *The Generation of Animals*, and *The Parts of Animals*, contain an immense body of facts, many of them singularly accurate, others as curiously incorrect, a circumstance which no one will wonder at who, with all modern resources at his elbow, has tried to break fresh ground in any department of Zoology. Although he propounds no definite system of classification, he clearly recognises many of the more important animal groups, or, as he calls them, "genera." Vertebrata, for instance, are spoken of as animals with blood (*ἔναιμα*) and Invertebrates as animals without blood (*ἄναιμα*), colourless blood not being recognised as such. Among animals with blood are included Viviparous Quadrupeds (Mammals), Birds, Oviparous Quadrupeds (Reptiles and Amphibia), Cetacea, and Fishes: among bloodless forms, Malakia or soft animals (Cephalopods), Malacostraca or soft animals with shells (the higher Crustacea), Entoma (Insects, Arachnids, Myriapods, and the higher Worms), and Ostracodermata or shelled animals (Echinoids, Cirripedes, Pelecypoda, Gastropoda, and Tunicata). Starfishes, Medusæ, and Sponges are also referred to.

In the then existing state of knowledge it was impossible that even so profound a philosopher as Aristotle could erect a science of Zoology. No standard of nomenclature was established; there was no clear idea of what constitutes a species: in matters of structure, no distinction was drawn between nerves and tendons: in physiology the vessels and tendons were looked upon as the organs of movement, the muscles being considered as mere packing. Obviously, anything like real progress was barred by ignorance of animal structure and function, and it was absolutely necessary that exact anatomical knowledge should precede anything approaching to successful generalisation.

It is, therefore, hardly to be wondered at that, up to the time of Ray, scientific Zoology owes more to those anatomists and physiologists whose main object was to advance the study of Medicine, than to the naturalists in the ordinary sense of the word. With the exception of the works of **Galen** (born A.D. 130), which contain numerous observations on the anatomy of Mammals, anatomy, as well as Zoology in the broad sense, was practically at a standstill from the time of Aristotle to the sixteenth century, when **Vesalius,** by his observations, chiefly on the human subject, raised anatomy to a degree of accuracy hitherto undreamt of; and **Coiter, Bellonius,** and **Fabricius ab Aquapendente** resumed the study of comparative anatomy, dormant since Aristotle. Somewhat later—in 1645—**Severino** published his *Zootomia democritæa*, the first book devoted exclusively to the general subject of comparative anatomy.

During the same period the general knowledge of animals was increasing, and a distinct epoch is marked by the learned, and, for the time, exhaustive *Historia animalium* of **Conrad Gesner,** published in 1551–58, and consisting of 4,500 folio pages, with numerous illustrations, some of them of considerable merit, some wonderfully inaccurate, some depicting various fabulous monsters, such as Winged Dragons, many-headed Hydras, and crowned Basilisks, the existence of which was not yet thoroughly discredited. The work is, however, rather an encyclopædia than the exposition of a science: it contains no general ideas; there is still no conception of the subordination of groups, and no exact naming either of animals as a whole or of their various parts. Five chief groups of animals are recognized: Viviparous Quadrupeds, Oviparous Quadrupeds, Birds, Aquatic Animals, and Serpents. Within these divisions the various animals are described without any attempt at grouping. Among Aquatic Animals, for instance, Fishes, Amphibia, Cetacea, Molluscs, Crustacea, Echinodermata, and Sea-serpents are included.

In the seventeenth century great strides were made both in knowledge of structure and function, in generalisation, and in methods of investigation. Especially famous and fruitful—indeed one of the greatest scientific events of all time—was the discovery of the circulation of the blood, made by **William Harvey** in 1616, and announced in 1628 in a small pamphlet *Exercitatio anatomica de Motu Cordis et Sanguinis.* He demonstrated fully, partly by dissections, partly by experiments on living animals, the action of the heart as a pumping mechanism, the nature of its valves and of those of the veins, the presence of blood,—not air, as was then supposed—in the arteries, the cause of the pulse, and the whole course of the circulation so far as it could be known previous to the discovery of the microscopic capillaries. Of hardly less importance is Harvey's embryological work: he made extended observations on the development of the Chick and in his *Exercitationes de Generatione Animalium* (1657) declared that all living things arise from a *primordium,* or ovum, and propounded the doctrine of *epigenesis* according to which development is a process of gradual differentiation of the primordium, whereby "out of the inorganic arises the organic, out of the similar the dissimilar." The primordium itself he considered might "proceed from parents, or arise spontaneously, or out of putrefaction."

Harvey worked with no optical aid beyond a simple lens, and it is not surprising that his results are incomplete and often inaccurate. His successors had the advantage of the compound microscope, invented by **Hans** and **Zacharias Janssen** about 1590–1600, and sufficiently improved during the course of the seventeenth century to be an important engine of research in the hands of the earliest microscopists, **Malpighi** in Italy, **Leeuwen-**

hoek and **Swammerdam** in Holland, **Robert Hook** and **Nehemiah Grew** in England. Malpighi made numerous histological discoveries, with some of which—such as the Malpighian capsules of the kidneys and the Malpighian vessels of Insects, his name is still associated. He was also the first to study the development of the Chick under the microscope, and was one of the earliest supporters of the theory of *pre-formation*,[1] according to which all the parts and organs of the adult are present in the germ, so that there is no differentiation, but only an unfolding. Leeuwenhoek discovered blood-corpuscles, striated muscle-fibres, dentinal canals, and epiderm-cells, observed the circulation of the blood in the Tadpole's tail, and described many of the lesser forms of life, such as Infusoria, Rotifers, and Hydra. Swammerdam investigated the anatomy of Insects and Molluscs, and the metamorphosis of Insects, and described the three "sexes" of Bees. The researches of Hook and Grew were mainly botanical; both they and Malpighi discovered in the tissues of plants little spaces with firm walls and full of fluid; these they called *cells*, thus taking the first step in the structural analysis of the higher organisms.

Another discovery of fundamental importance was made in 1677 when **Louis de Hamen** observed and described the sperms of animals. These were at first thought to be the young, which only required to be nourished in the egg to grow into the embryo or fœtus, and were therefore considered to disprove the theory of the *ovulists*, such as Harvey, who made the egg the origin of the new generation, in favour of that of the *spermatists*, who believed the whole material to be furnished by the male parent.

Belonging also to this period are **Redi's** experiments on generation, in which he began the work of establishing the doctrine of *biogenesis*, according to which organisms originate only from pre-existing organisms, and of demolishing that of *abiogenesis*, or "spontaneous generation," which, maintained from the time of Aristotle onwards, held that Flies, Lice, Worms, and other animals were directly generated in mud, putrefying flesh, dung, etc., having, therefore, no living progenitors. Redi's contribution to this question lay in proving, for the first time, that the maggots, "bred" in putrefying meat, were the products of eggs laid thereon by Flies.

Thus the seventeenth century saw a great advance in the knowledge of animal structure and function, and the way was paved towards a rational classification. As we have already seen, **Ray,** towards the end of the century, gave zoology as a whole a scientific form; he first grasped the ideas of species and of specific characters, acknowledged anatomy as the basis of classification, and introduced a greatly increased precision in the definition of species and other groups, and in terminology. He had, however,

[1] Often known as the theory of *evolution*. As, however, the latter word is now universally used in a different sense, it is advisable to drop it in this connection, and to employ the synonym pre-formation.

no clear idea of genera, his genera being rather what we now call orders or families, and he showed an undue conservatism in retaining, as far as possible, the groups of Aristotle. His general classification of animals is as follows:—

I. Animals with (red) blood [*Vertebrata*].
 1. Respiration pulmonary.
 A. Heart with two ventricles.
 (*a*) Viviparous.
 i. Aquatic [*Cetacea*].
 ii. Terrestrial [*other Mammalia*].
 (*b*) Oviparous [*Birds*].
 B. Heart with one ventricle.
 Viviparous Quadrupeds and Serpents [*i.e. Reptilia* and *Amphibia*].
 2. Respiration branchial [*Fishes*].

II. Animals without (red) blood [*Invertebrata*].
 1. Majora.
 A. Mollia [*Cephalopoda*].
 B. Crustacea.
 C. Testacea [*Gastropoda* and *Pelecypoda*].
 2. Minora.
 Insecta [*Insecta, Arachnida Myriapoda*, and *Vermes*].

It will be noticed that, while the classification of Vertebrates is fairly natural, being founded upon the rock of Anatomy, the arrangement of Invertebrates is no advance upon that of Aristotle: the two main divisions depend upon mere size, and Crustacea, separated from the rest of the Arthropoda, are interposed between Cephalopods and the remaining Mollusca. In association with Ray must be mentioned his friend and fellow-worker **Francis Willughby,** who made extensive contributions to Zoology.

The eighteenth century saw the imperfect efforts of Ray developed, and in some respects perfected, by Carl Linné or **Linnæus**, universally recognised as the founder of modern systematic Zoology—or more accurately Biology, since his reforms equally affected Botany. Born in Sweden in 1707, two years after Ray's death, he published the first edition of his *Systema Naturæ*, in 1735, as a small pamphlet. The twelfth edition (1766–68) was in three volumes, and was the last to receive the author's corrections, but from materials left at his death in 1778 an authoritative (thirteenth) edition in ten volumes was prepared by **J. F. Gmelin.**

It was Linnæus who first recognised the value of groups higher than species—genera, orders, classes, etc., and employed them

in a definite and uniform way, with due subordination of one to the other; it was he who invented *binomial nomenclature*, the advantage of which in promoting precision in systematic work it is impossible to over-estimate. He gave each species a brief diagnosis in Latin, so that any naturalist versed in his system could recognise whether an animal or plant which came under his notice was already described or not. In this way he, as it were, pigeon-holed the facts of Biology, and so made the determination of the proper place of any new fact a comparatively simple matter. By universal consent, the *Systema Naturæ* is taken as a starting point by systematists. It is customary to place after the name of a species the initial or abbreviated name of the writer by whom the species was first distinguished and named. For instance, the Bass, a common British Teleost, was named *Perca labrax* by Linnæus. In 1828, Cuvier and Valenciennes, in their great work on Fishes, recognised that it was generically distinct from the Perch, and, retaining the generic name *Perca* for the latter, called the Bass *Labrax lupus*. In 1860, further investigations into the Perch family necessitated placing it in the genus *Morone*, and, according to the law of priority, the specific name *lupus* gives place to *labrax*, the latter having been applied by Linnæus. The Bass is therefore correctly called *Morone labrax*, Linn., the more usual name, *Labrax lupus*, Cuv. and Val. becoming a synonym. In deciding all such questions of priority, the tenth edition (1758) of the *Systema Naturæ* is taken as a starting point: all species distinguished by Linnæus, and not subsequently split up into two or more species, are distinguished by the abbreviation *L.* or *Linn.* For instance, *Canis familiaris Linn.* is the Domestic Dog, *Passer domesticus Linn.* the House Sparrow: and names given by the older naturalists are neglected unless endorsed by Linnæus.

In many respects the system of Linnæus was eminently artificial; he relied too much on single characters in classification, and did not take the totality of structure into sufficient consideration. He divided the animal kingdom into the following six classes:—

1. Mammalia.
2. Aves
3. Amphibia [including *Reptilia* and *Amphibia*].
4. Pisces.
5. Insecta [including all the *Arthropoda*].
6. Vermes [including *Mollusca*, *Worms*, *Echinoderms*, *Cœlenterata*, and *Protozoa*].

It will be seen that all these classes are natural groups, with the exception of the last, but that they are far from being of even approximately equal value. The first four are what we still call classes, but there is no attempt to unite them into a single group of higher order; and in this respect the classification of Linnæus

falls behind that of Ray, who recognised the phylum Vertebrata under the name of animals with blood. The fifth class, on the other hand—that of Insecta—is the equivalent of an entire phylum, while under the head of Vermes are included all the phyla recognised at the present day, except Chordata and Arthropoda.

Other naturalists of the eighteenth century must be briefly referred to. **Bonnet** introduced the idea of a "scale of beings" (*échelle des êtres*), conceiving the true classification to be a linear one, passing in a single series from the lowest to the highest forms. This conception was opposed by **Pallas**, who introduced the true conception of representing the relationships of the various groups under the form of a much branched tree. **Spallanzani** made numerous investigations on reproduction, and, together with Bonnet, Buffon, and Haller, strongly supported the doctrine of pre-formation already referred to. **Haller** summed up the position by stating emphatically that there was no such thing as development or differentiation, no part of the body being made before another, but all parts simultaneously created. It followed, as a natural corollary from this view, that the germ destined to give rise to an animal—*i.e.*, the ovum according to the ovulists, the sperm according to the spermatists—contained within itself the germ of the next generation, that of the next, and so on, *ad infinitum*, so that the first created male or female of each species contained within its sperms or ova the germs of all future generations, enclosed one within the other, like a nest of Chinese boxes. **Buffon**, as the result of numerous experiments, came to the conclusion that the ovary secretes a seminal fluid containing moving particles analogous to sperms, and, from this erroneous observation, framed a theory which is an interesting anticipation of Darwin's Pangenesis (p. 625), namely, that organic particles, derived from all parts of the body, occur in the seminal fluids of the two sexes, and that the union of these in the uterus "determines them to arrange themselves as they were in the individuals which furnished them."

The theory of pre-formation was practically demolished, and that of epigenesis, or new formation, established on a firm basis, by **Caspar Friedreich Wolff**, who, at the age of twenty-six—in 1759—gave the most accurate account of the development of the Chick hitherto known, and showed clearly that there was no pre-formation of the various parts, but a gradual differentiation from a layer of organised particles, or, as we should now say, from a cellular blastoderm.

Another great eighteenth century name is that of **John Hunter**, the most profound comparative anatomist and physiologist of his time. He was not a zoologist in the narrow sense of classifier, but his exquisite investigations on the various systems of organs and their functions throughout the animal kingdom furnished the science with a foundation of wide and exact knowledge which was

of far more importance than the most cunningly devised system of classification. Important anatomical investigations were also made during this period by **Vicq d'Azyr**, who enunciated the principle of serial homology; by **Peter Camper**, who investigated the pneumaticity of the bones of Birds, and was the first to apply exact methods of measurement to the human skull; by **Alexander Monro**, who greatly advanced our knowledge of the anatomy of Fishes; and by **Poli**, whose *Testacea utriusque Siciliæ* is the most famous of the older works on Mollusca. And in the domain of out-door zoology—the study of the actual life of animals with but little regard to their structure or classification, or to the broader scientific questions connected with them—special mention must be made of **Gilbert White**, whose *Natural History and Antiquities of Selborne* is a classic both in science and letters.

The latter part of the eighteenth century is also specially remarkable for the publication of the earliest scientific speculations on the origin of species. The idea of evolution is to be found in the works of more than one of the great Greek and Roman philosophers, such as **Empedocles** (495—415 B.C.), and **Lucretius** (99—55 B.C.); and the writings of some of the Fathers of the Church, such as **Augustine** (353—430) and **Thomas Aquinas** (1225—1274) seem to show that they had no objection to "derivative creation," or evolution under direct Divine superintendence. But by about the middle of the sixteenth century, the idea of the immutability of specially created species had hardened into a dogma which it was unsafe to question; and, this state of things continuing, the earliest of the great evolutionists, **Buffon**, felt himself obliged to qualify all his speculations with a declaration, sincere or ironical, of his belief that species were immutable. Linnæus, reckoning all higher groups as subjective, contended for the real existence of species, saying "we recognise as many species as were originally created," and this opinion was held by the vast majority of naturalists, not only of his own time, but up to within thirty or forty years of the present day.

Buffon, born in the same year (1707) as Linnæus, was, in his methods and ideas, the exact opposite of his great systematising contemporary. He wrote charming accounts of the external characters and habits of animals, but declined to classify them, on the ground that all arrangements of the kind were arbitrary and that it was easier, more useful, and more agreeable to consider the lower animals in relation to ourselves. On this principle, he begins his *Histoire naturelle* with Man, then takes up the various domestic Mammals, and afterwards proceeds to consider the less familiar forms. But he was essentially a philosophical zoologist; besides, enunciating a theory of heredity, he grasped the idea of homology, endeavoured to explain the facts of geographical distribution, and in a tentative and guarded way admitted the mutability of species, and advanced a hypothesis

of their origin. His speculations refer mainly to the modification, or, as he calls it, degeneration, of domestic animals, and he sums up his position as to the factors of the process by saying "the temperature of the climate, the quality of nutriment, and the ills of slavery, these are the three causes of change, of alteration, and of degeneration in animals." In other words, he supports the theory of the direct action of the environment.

A bolder and more consistent evolutionist than Buffon was his contemporary, **Erasmus Darwin** (1731—1802), grandfather of the author of the *Origin of Species*. As a competent critic has said, "he was the first who proposed and consistently carried out a well-rounded theory with regard to the development of the living world." In his *Zoonomia*, published in 1794–6, after summarising the extraordinary adaptations to be seen in the animal kingdom, he asks, "Would it be too bold to imagine that all warm-blooded animals have arisen from one living filament [he was a spermatist] which the great First Cause endued with animality, with the power of acquiring new parts, attended with new propensities, directed by irritations, sensations, volitions, and associations; and thus possessing the faculty of continuing to improve by its own inherent activity, and of delivering down those improvements by generation to its posterity, world without end?" And a little later he inquires: "Shall we conjecture that one and the same kind of living filament is and has been the cause of all organic life?" He anticipated Lamarck in the importance he attached to the principle of use and disuse, expressed his belief in the inheritance of acquired characters, and recognised the importance of sexual selection.

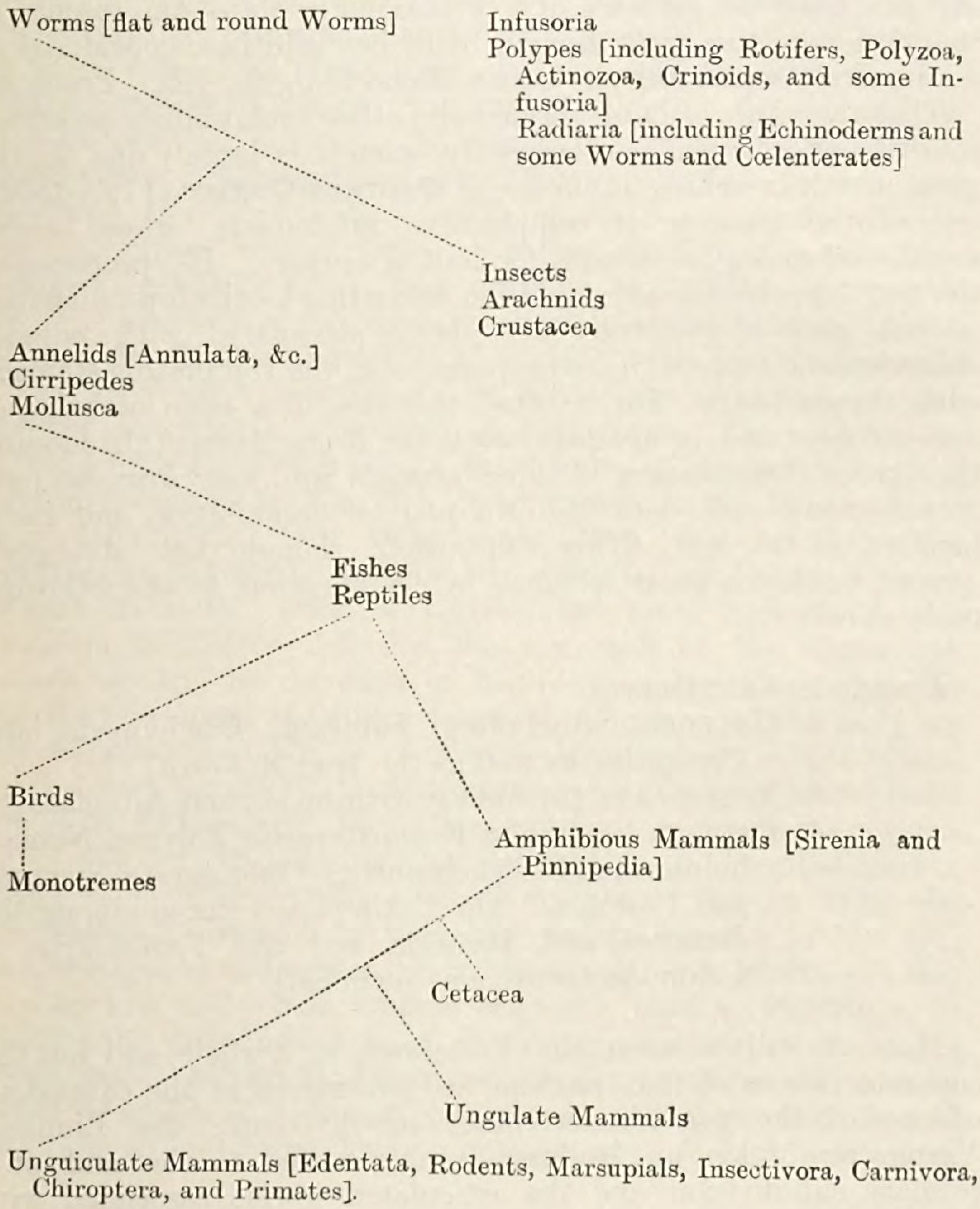
The study of Zoology was also greatly advanced during the eighteenth century by the voyages of **Cook**, **Bougainville**, and others. New countries were explored, the peculiarities of their faunæ recorded, and valuable data accumulated for the study of distribution. In this connection the names of **Sir Joseph Banks**, **Solander**, and the two **Forsters**, all attached to Cook's expeditions, of **Sparrmann**, and of **Sir Hans Sloane**, may be specially mentioned. The last-named was one of the greatest of collectors, and the founder of the British Museum.

The beginning of the nineteenth century was a period of great zoological activity, distinguished by the work of some of the most prominent leaders of the science.

J. B. P. A. de Lamarck (1744–1829) was not only a distinguished general zoologist and palæontologist, but may also be looked upon as the chief of the pre-Darwinian evolutionists. In his *Philosophie Zoologique*, published in 1809, he completely rejected the idea of the fixity of species, and endeavoured to explain the transformation of one form into another by the operation of known causes; of these he attached most importance to the principle of use and disuse, and he was a firm believer in use-inheritance. He was a

uniformitarian in Geology, believing that the history of the earth and of its past inhabitants is to be explained by the action of the causes seen in operation to-day, and not by invoking great catastrophes or cataclysms by which changes of vast magnitude were suddenly produced. He considered, also, that the transformation of species took place by slow, orderly changes, Nature requiring only matter, space, and time in order to effect her various changes. He introduced the terms Vertebrata and Invertebrata, and, in the same year as **Treviranus** (1802) proposed the term *Biology* for the whole science of living things.

Lamarck at first believed in a linear classification of animals, but afterwards adopted the earliest known branching or phylogenetic classification—a crude attempt, but interesting as being the first of its kind. It is as follows :—



The hypothesis of evolution was also supported by Lamarck's contemporary, **Etienne Geoffroy St. Hilaire**, who denied use-inheritance and considered the direct action of the environment as the sole cause of transformation. He also differed from Lamarck in believing in the occurrence of sudden changes, *e.g.*, in the possibility of the emergence of a fully-formed Bird from a Reptile's egg. In systematic zoology he established the orders Monotremata and Marsupialia: the members of the latter group had hitherto been distributed among Rodents and Primates.

Another keen supporter of evolution was the great poet **Goethe** (1739–1832), who also introduced the word *Morphology*, and made important contributions to the department of science thus named. He propounded the vertebral theory of the skull, presently to be referred to (p. 640), recognised the importance of vestigial organs, and predicted the presence of a premaxilla in Man—the absence of that bone in the adult human skull being hithero considered as distinctively separating the genus Homo from the other Primates.

That the views of Lamarck and the other evolutionists produced so little effect upon contemporary science is largely due to the great and far-reaching influence of **Georges Cuvier** (1769–1832), one of the greatest of comparative anatomists, whose views dominated zoological science for half a century. He propounded the fruitful principle of correlation, according to which peculiarities in one part of the body are always associated with equally characteristic features in other parts—*e.g.*, the ruminating stomach with cloven hoofs. He rejected the idea of a scale of being or unity of type, and, in his great work, the *Règne Animal*, abandoning the linear classification, divided animals into four *Branches* (*embranchemens*), each with its own plan of organisation and independent of the rest. This conception, though not absolutely correct, marked a great advance in classification, as the following table shows.

Branch 1. VERTEBRATA.
„ 2. MOLLUSCA [including Tunicata, Brachiopoda, and Cirripedia, as well as the true Mollusca].
„ 3. ARTICULATA [including Arthropoda and Annulata].
„ 4. RADIATA [including Echinodermata, Polyzoa, Nemathelminthes, Platyhelminthes, Cœlenterata, Sponges, and Protozoa. The Rotifera are placed among the Protozoa, and Bacteria and the Pedicellariæ of Echinoderms are also included].

Here, it will be seen, the Vertebrata as a whole, and not the separate classes of that phylum, are considered as the equivalent of one of the great invertebrate sub-divisions: the Linnæan Vermes are broken up, Mollusca being elevated to the rank of a primary sub-division, and the articulated worms associated with

Arthropods; while Echinoderms are grouped with Cœlenterata on account of their radial symmetry, and the imperfectly understood lower Worms, Sponges, and Protozoa are included in the same branch.

Cuvier may also be said to have created the science of Palæontology by his investigation of the Tertiary Mammalia of France. As long ago as the sixth century B.C., **Xenophanes** had recognised fossils as the actual remains of animals, but the usual view was that they were merely mineral productions; and one of the earliest observers in modern times to perceive their true nature was **Scheuchzer**, at the beginning of the eighteenth century, who considered them as evidences of a universal deluge. Cuvier, as well as the English geologist **William Smith** (1769—1839), showed that the older fossils belonged to entirely different species, genera, and even families, from the animals existing at the present day, the differences being greater in the deeper than in the more superficial formations. In this way the idea of a definite succession of life in time was introduced. Cuvier and his followers rejected, however, the notion of any genetic connection between the inhabitants of successive geological periods, and considered that the fauna of each epoch was exterminated by some cataclysm or convulsion of nature, and the earth subsequently re-peopled by a fresh creative act. This catastrophic view of the history of the earth received its death-blow in 1830—33, when **Sir Charles Lyell** (1797—1875) published his *Principles of Geology*, next to the *Origin of Species* the most famous contribution to natural science in modern times. By insisting on the evidences for continuity in the history of the earth, he prepared men's minds for the idea of continuity in the history of its living inhabitants, and thus, more than any of the older evolutionists, paved the way for the reception of Darwin's views.

Apart from the work of Cuvier, the most important contributions to Zoölogy during the first half of the nineteenth century are in the domains of histology and embryology. In 1838 the *cell-theory*, according to which all parts of the body are built up either of cells or of tissues derived from cells, was propounded first for plants by **Schleiden**, and shortly afterwards for animals by **Schwann**. Both, however, had an erroneous conception of the cell, considering the cell-wall as its essential part—whence the name *cellula*, a small chamber. But in 1846 the "plant-slime," observed by Schleiden in the interior of the cell, was investigated with great thoroughness by **von Mohl**, and was called by him *protoplasm*, a name originally used by **Purkinje,** in 1840, for the substance of which the youngest embryos of animals are composed. **Albert Kölliker** and others proved that animal cells existed in which no cell-wall was present, and **Dujardin** showed that Amœbæ and other lowly organisms were formed entirely of

protoplasm, or, as he called it, *sarcode*. These discoveries paved the way for the generalisations of **Max Schultze** and **De Bary**, that the essential constituent of the cell is protoplasm, and that the protoplasm of animals and plants is identical.

In embryology, the most important work of this time was that of **K. E. von Baer**, who, in 1827, discovered the ovum of Mammals. He also described the three primary germ-layers—ectoderm, mesoderm, and endoderm—in the Vertebrate embryo, and showed that histological differentiation, or the formation of the permanent tissues from embryonic cells, proceeds hand in hand with morphological differentiation or the evolution of organs. He was thus led to enunciate what is known as *von Baer's law*, that development is a progress from the general to the special, and to frame the generalisation that embryos of animals belonging to various classes closely resemble one another in their earlier stages, but diverge more and more as development proceeds. His investigations led him to support Cuvier's view of the division of the animal kingdom into distinct and clearly separated types or branches.

It was during this period also that the real meaning of fertilisation was discovered, and the controversy between ovulists and spermatists finally set at rest. Artificial fertilisation had been tried in the last century, but up to 1842 the greatest physiologist and most accurate anatomist of his time, **Johannes Müller**, was unable to state positively whether or not the sperms were parasitic animalcules. But in 1843 **Martin Barry** observed the union of ovum and sperm in the Rabbit, and three years later **Kölliker** proved that the sperms were developed from the cells of the testis.

The period under consideration also saw the development of a school of speculative or deductive zoology. In 1790 **Goethe** conceived the idea that the skull of Vertebrates is made of modified vertebræ—in other words, that the skull is the highly differentiated anterior end of the backbone. This theory, which may be taken as a type of morphological speculation in the pre-evolutionary period, was re-enunciated and greatly elaborated in 1807 by **Lorenz Oken**, whose conclusions are worthy of mention, if only to show the dangers of the deductive method in natural science, and the lengths to which unbridled speculation may carry a presumably sane man. He did real service by demonstrating the secondary segmentations of the bony skull; the occipital segment being his "ear vertebræ," the parietal his "jaw vertebræ," and the frontal his "eye vertebræ." But he clearly went beyond the limits of legitimate speculation when he contended that the nasal cavity is a cephalic thorax and the mouth a cephalic abdomen; that the bones of the upper jaw are homologues of the fore-limbs, the lower jaw of the hind-limbs, and the teeth of the digits.

About the middle of the century the vertebral theory, freed from the most obvious absurdities of Oken, was resuscitated and developed by **Sir Richard Owen** (1803–93) in his *Report on the Archetype and Homologies of the Vertebrate Skeleton*, published in 1846. He also founded his generalisations on the structure of the adult or late embryonic skeleton in the higher groups, neglecting the unsegmented crania of Cyclostomes and Elasmobranchs, and of the higher Vertebrate embryo. In his view, the limb-girdles are modified ribs, the shoulder girdle belonging to the "occipital vertebra," while the limbs themselves are "diverging appendages," or uncinates.

Owen's chief services to Zoology were, however, his numerous and brilliant anatomical researches, such as those on Nautilus, on Apteryx, and on the structure and homologies of the teeth in the entire vertebrate series; and his palæontological investigations, especially those on Archæopteryx, on the fossil Mammals of Australia, and on the Dinornithidæ, and other flightless Birds. His conclusion from the examination of a single fragmentary femur, that there had existed in New Zealand a Bird larger and heavier than the Ostrich—a fact then practically unknown—forms one of the most famous stories in natural history. His contributions to classification were not happy; he took the nervous system as the basis of his larger divisions, classifying Mammals, for instance, according to the presence or absence of a corpus callosum, and of convolutions, and placing Man in a separate sub-class as the supposed sole possessor of a posterior cornu and hippocampus minor. He rendered great service to philosophical Zoology by pointing out the distinction between homology and analogy, and by the publication of his great text-book on the *Anatomy and Physiology of Vertebrates*.

The chief successor of Cuvier in France was **Henri Milne-Edwards** (1800–18), who enunciated the principle of the division of physiological labour, and modified the classification of Cuvier in several particulars. He separated Tunicates from Mollusca proper, and united them with Polyzoa under the name of *Molluscoida*, and he divided Vertebrates into *Allantoidea* and *Anallantoidea*, according to the presence or absence of an allantois; in so doing he took the important step of separating Amphibia from Reptiles, a step in which **De Blainville** had been his only precursor. His learned *Leçons de l'Anatomie et de la Physiologie comparée* is a storehouse of information on the structure and functions of animals.

It was not until about the middle of the century that further increase in the knowledge of the lower animals resulted in the gradual dismemberment of Cuvier's unnatural Branch Radiata. **Frey** and **Leuckart** established the group Cœlenterata, and placed Echinoderms apart; **Wiegmann** removed Rotifera from

Protozoa to Vermes; **Vaughan Thomson** defined the Polyzoa, and **Rudolphi, Leuckart,** and **von Siebold** showed that the Flat-worms were in no sense Zoophytes. Sponges were considered by some as polypes, by others as plants; the current of water setting in at the pores and out at the oscula was discovered by **Robert Grant** about 1820: later, **Bowerbank** demonstrated the presence of cilia, and the full proof of their animal nature was made by the researches of **Lieberkühn** and **Carter**. The Foraminifera were classed as Cephalopoda until the thirties, when **Dujardin** determined their proper place by the discovery of the living protoplasmic body. Other important advances in classification were the separation of Cirripedia from Mollusca by **Vaughan Thomson**, and the withdrawal from intestinal worms of the parasitic Copepoda and of the Pentastomida. The Infusoria have also had a chequered history. **Ehrenberg** in his magnificent work *Die Infusionsthiere*, looked upon the food-vacuoles as stomachs, and described a complex enteric canal connecting them; it is, therefore, not surprising that he considered them as belonging to the same group as Rotifers. **Louis Agassiz,** as late as 1859, considered Paramœcium, Opalina, &c., to be the young of Planarians and Trematodes, and Vorticella to be a Polyzoan, and it was only by the researches of **Stein** and others that the class of Infusoria was fully established as a natural group of unicellular organisms.

The Swiss zoologist, **Agassiz** (1807–73), referred to in the preceding paragraph, is interesting, not only as one of the foremost naturalists of his time and the founder of the large and active school of zoologists in the United States, where he spent the latter part of his life, but also as the last great biologist to maintain the fixity of species. In his *Essay on Classification*, published, curiously enough, in the same year (1859) as the *Origin of Species*, he supports the proposition that the various subordinate groups of animals, from phyla to species, are not mere "devices of the human mind to classify and arrange our knowledge in such a manner as to bring it more readily within our grasp and facilitate further investigations," but that they "have been instituted by the Divine Intelligence as the categories of His mode of thinking." In other words, that in our classifications we "have followed only, and reproduced, in our imperfect expressions, the plan whose foundations were laid in the dawn of creation."

In 1859 occurred what may fairly be called the most important event in the history of biological science, the publication of **Charles Darwin's** *Origin of Species*. The evolutionary theories of Buffon, Erasmus Darwin, Lamarck, and Geoffroy St. Hilaire had produced little effect upon contemporary zoology; and **Robert Chambers's** *Vestiges of Creation* (1844), although exciting

great interest, was too crude and speculative to make many converts among men of science. But Darwin had the advantage of being, not only a philosopher, but a naturalist in the broadest sense—a systematist with a sufficient knowledge of anatomy, thoroughly conversant with the breeding of domestic animals and cultivated plants, a keen observer of external nature, both organic and inorganic, and with unrivalled experience as a traveller. It is not surprising, therefore, that the wealth of illustration, the close reasoning, and the philosophic spirit of the *Origin*, converted the whole scientific world to the general doctrine of transformism within twenty years. The theory of Natural Selection, the Survival of the Fittest, or the Preservation of Favoured Races in the Struggle for Life, was first grasped by Darwin in 1838, but was not published until 1858, when it was announced simultaneously by himself and by **Alfred Russel Wallace**. Both these authors had, however, been anticipated by **W. C. Wells** in 1813, and by **Patrick Matthew** in 1831. Darwin's other works, especially *The Variations of Animals and Plants under Domestication* and *The Descent of Man*, rank among the most important contributions to philosophical Biology. With them must be mentioned the luminous *Principles of Biology* of **Herbert Spencer,** who has consistently upheld the direct action of the environment as a factor in evolution. Wallace, on the other hand, is a pure selectionist, while Darwin held "that natural selection has been the main but not the exclusive means of modification."

The additions to zoological knowledge made by the voyagers of the eighteenth century have been referred to; even more important are the numerous great scientific expeditions of the nineteenth. Among the most prominent of these are the voyages of the French ships *Astrolabe*, *Uranie*, *Bonite*, and *Géographe*, in which researches were carried on by **Peron** and **La Sueur, Quoy** and **Gaimard, Eydoux** and **Souleyet,** and **Hombron** and **Jacquinot,** and given to the world in splendidly illustrated folios. Still more famous is the voyage of H.M.S. *Beagle* (1831–36), in which Darwin gained his extraordinarily wide and accurate knowledge of natural history, and the narration of which is published in his *Naturalist's Voyage*. Other celebrated voyages are those of H.M.S. *Rattlesnake* (1846–50), of which **T. H. Huxley** was assistant-surgeon; of H.M.SS. *Erebus* and *Terror*, accompanied by **Sir J. D. Hooker;** of the American "Wilkes" expedition, with **J. D. Dana** as naturalist, and of the Austrian frigate *Novara*. But the most famous and complete of all scientific voyages was that of H.M.S. *Challenger*, in 1872–76, the five years' cruise of which was marked by discoveries of great importance by the scientific staff, **Sir Wyville Thomson, John Murray, H. N. Moseley,** and **Willemoes-Suhm**, while the zoological material col-

lected on the voyage was worked out by the leading zoologists in all parts of the world, and the results published in thirty handsome and fully illustrated quarto volumes.

In land-travel numerous journeys, and especially those of **A. R. Wallace** in the Malay Archipelago and Brazil, and of **H. W. Bates** in Brazil, have not only added immensely to our knowledge of the genera of the countries visited, but have enriched the science with the ideas of protective and aggressive characters, of mimicry, and of the relations of organism to environment generally.

The establishment of Zoological Gardens in different parts of the world—notably in Paris and London—has added greatly to our knowledge both of the habits and of the anatomy of animals, and a similar advance in the investigation of marine animals has followed upon the establishment of Zoological Stations or Marine Laboratories in various countries. The earliest and most important of these is the Naples Station, founded in 1870 by **Anton Dohrn**. The results of the researches there carried on form the most elaborate and sumptuous series of zoological monographs ever published.

The establishment of Zoological (or Biological) Laboratories in connection with Universities is also a work of the last five and twenty years, and has had an important influence both in diffusing a knowledge of the science and in stimulating research. Even more recent is the complete change of view as to the functions and arrangement of a Museum. Formerly it was looked upon as a collection of curiosities, in which everything was to be exhibited to the public. Now, thanks in great measure to **Sir W. H. Flower** in England, and **Brown Goode** in America, special collections are formed for study and research, while the cases accessible to the public are gradually becoming a series of actual illustrations of zoological science, in which not only the principles of classification, but the chief facts of structure, life-history, and habit are strikingly and adequately shown.

During the second half of the present century, Zoology as a whole has been greatly influenced by the writings of **Thomas Henry Huxley** and of **Ernst Haeckel**. Huxley (1825–1895) was the first to point out the homology of the ectoderm and endoderm of Cœlenterates with the two primary germ-layers of the vertebrate embryo. He also introduced the word *zooid*, demolished the vertebral theory of the skull, and placed the anatomy of the fossil Ganoids upon a satisfactory footing, as well as making many other important contributions to animal morphology. His *Elements of Comparative Anatomy* (1864) forms an important landmark in the history of modern Zoology, as giving the views of one of the keenest, most logical, and least speculative of biologists just before the time when the various improved histological and

embryological methods began to revolutionise the science. Huxley's "eight primary categories or groups" are as follow :—

VERTEBRATA.

MOLLUSCA.

MOLLUSCOIDA [including Brachiopoda, Polyzoa and Tunicata].

CŒLENTERATA.

ANNULOSA [including Arthropoda and Annulata].

ANNULOIDA [including Echinodermata, Rotifera, Platyhelminthes and Nemathelminthes].

INFUSORIA [including Infusoria proper and Mastigophora].

PROTOZOA [including Rhizopoda, Sporozoa, and Porifera].

The lower "Worms" are associated with Echinoderms, on account of the resemblance of the adult Rotifers, as well as of the larvæ of certain Flat Worms to the echinopædium. Sponges are placed among the Protozoa, in accordance with the view that they are to be looked upon as colonies of unicellular zooids. Infusoria are separated from the remaining Protozoa, because conjugation was misinterpreted as a true sexual process, the mega-nucleus being considered as an ovary, the micro-nucleus as a testis.

Haeckel, apart from his elaborate and beautiful researches on the Radiolaria, Calcareous Sponges, and Hydrozoa, is remarkable as the first modern zoologist to attempt the classification of animals on a frankly evolutionary basis. We owe to him the terms phylogeny and ontogeny, cœnogenesis and palingenesis, and the fruitful "gastræa-theory," according to which the gastrula is the ancestral form of all the Metazoa. His classifications take the form of genealogical trees, and he was the first to employ the method of introducing hypothetical ancestral forms, wherever they might be wanted to complete the connection between known groups. He may be said, in fact, to have founded a school of deductive zoology, the phylogenetic speculations of which are often as ingenious and suggestive as they are transient. The student must, however, bear in mind that Archi-molluscs, Ideal Craniates, and Pro-mammalia are mere figments of the imagination, and have no more real existence than the "Divine Archetypes" of an earlier school of thought.

One result of the new views on species, very obvious in the writings of both Huxley and Haeckel, was the marked alteration in the position assigned to Man in the animal series. **Linnæus** considered *Homo* as a genus of his order Primates, equivalent to Simia, Lemur, &c.; but **Cuvier** took the retrograde step of erecting a distinct order, *Bimana*, to contain Man alone, the Apes and

Lemurs forming the order *Quadrumana*. **Ehrenberg** went further, and divided the Animal Kingdom into *Nations, i.e.,* Mankind, and *Animals*. Even as late as 1857 **Owen**, as we have already seen, made a distinct sub-class, *Archencephala*, for Man, the remaining Primates being included with the other higher mammalian orders in the sub-class *Gyrencephala*. This view of the isolated position of Man was connected with the theory of his late appearance in time, and the fact of his co-existence with the Mammoth and other extinct Mammals, first proved by **Boucher de Perthes** in 1836 by the discovery of flint axes 20–30 feet below the present surface, was for many years almost universally denied. But **Lyell's** *Antiquity of Man* (1863) placed the geological evidence on a sound footing, and the same was done for the morphological evidence by **Huxley**, who, in his *Man's Place in Nature* (1863), summed up the position by the statement, now universally conceded, "that the structural differences which separate Man from the Gorilla and the Chimpanzee are not so great as those which separate the Gorilla from the lower Apes." Finally, **Darwin**, in his *Descent of Man* (1871), discussed the question from every point of view, and concluded that "Man still bears in his bodily frame the indelible stamp of his lowly origin."

It was also during the third quarter of the century that the old doctrine of Abiogenesis or Spontaneous Generation, first assaulted by Redi, but maintained by many naturalists from Aristotle to Haeckel, was finally disposed of. The accurate methods of **Louis Pasteur**, **Lord Lister**, **John Tyndall**, and others, proved conclusively that the Bacteria, Monads, and other lowly organisms which occur in putrefying substances do not arise *de novo*, but are the product of germs in the floating dust of the air by the exclusion of which putrefaction may be absolutely prevented.

During the last quarter of a century the progress of Zoology has been profoundly influenced by the improvements in microscopical methods, especially by the invention and perfection of the microtome, the method of serial section-cutting, and the various ways of preserving, imbedding, and staining tissues. The microtome began as a simple contrivance for holding small objects firmly while sections of them were cut by hand with a razor or other knife, and has developed into the various modern forms of the instrument in which the knife is fixed in a plane parallel to the surface of the object, and the latter is raised mechanically by small and equal increments as the sections are cut. In this way perfectly regular sections are obtained of an even thickness not exceeding the diameter of a cell. The method of imbedding began by simply holding an object, too small or too soft to be grasped by the fingers, between two pieces of carrot or pith, and

has gradually been evolved into the present method of complete impregnation with paraffin or celloidin, by means of which imbedding material and object form a homogeneous mass. Simple preservation in alcohol has given place to elaborate fixing methods by means of chromic, picric, or osmic acids, platinum chloride, corrosive sublimate, etc., and gradual hardening in alcohols of increasing strength. Similarly, direct staining with an ammoniacal solution of carmine has developed into innumerable methods of differential staining, mostly with aniline dyes, by which the various tissues and the constituents of the cell—chromatin, centrosomes, etc.—are clearly brought into view. By the serial method successive sections of an embryo or small animal are mounted in regular order so that the organs, tissues, etc., can be traced throughout the series. In this way the dislocation of parts produced by dissection is avoided, organs are seen in absolutely natural relations, and parts quite undiscernible either by dissection or by microscopic examination of the whole animal or of dissociated parts of it, are clearly brought into view. Morphological inquiry has, in fact, been brought within measurable distance of a precision limited only by the imperfections of our eyes and optical instruments. Similar accuracy in the topographical anatomy of the larger Animals, including Man, has been attained by freezing the whole subject and cutting it into sections with a saw.

These improved methods have necessitated a re-examination by their aid of every group in the animal kingdom, and, as a result, our knowledge of the structure of many Animals, especially of the lower forms, of complex organs such as the vertebrate brain, of embryology, and of the minute structure of cells and tissues has been completely revolutionised. Specially remarkable is the advance in our knowledge of the Sponges, Actinozoa, Echinoderms, and Amphioxus. The discovery of the unsuspected chordate affinities of Balanoglossus, Rhabdopleura, and Cephalodiscus is also worthy of special mention. Probably the greatest of comparatively recent embryological triumphs, belonging to the earlier part of the period now under discussion, is **Kowalewsky's** discovery of the notochord and hollow nervous system of the Tunicate larva, which resulted in the removal of the Urochorda from Molluscoida to Chordata, and in breaking down the sharp line between Vertebrates and Invertebrates.

But perhaps the most remarkable result of improved microscopical technique is the rise and development of a distinct department of histology, known as *cytology*, dealing with the minute structure of the protoplasm and nuclei and the various intra-cellular phenomena such as mitosis. Our knowledge of this subject is entirely a product of the last twenty years, and is due in great measure to the researches of **W. Flemming**, **E. Strasburger**,

and **E. van Beneden**. A modification of the cell-theory has also been necessitated by the proof that many animal tissues do not consist of distinct cells but of a continuous mass of protoplasm with more or less regularly arranged nuclei, and are therefore strictly not multicellular but *non-cellular*. As certain Protozoa, such as the Mycetozoa and Opalina, are also non-cellular, containing numerous nuclei in an undivided mass of protoplasm, the distinction between Protozoa and Metazoa appears to be less absolute than has hitherto been considered.

The advance in palæontology during the same period has also been immense. In particular, the researches of **E. D. Cope**, **O. C. Marsh**, and others in America have added whole orders to Zoology—the Odontolcæ, Ichthyornithes, Stereornithes, Amblypoda and Dinocerata—and have resulted in the discovery of many new and strange forms among the Dinosauria, Elasmobranchs, Ganoids, and other groups, and in the tracing of the pedigree of the Equidæ, Camelidæ, and other Mammalian families. Important, though less striking, discoveries have also been made among the fossil faunæ of Europe, India, South Africa, and Australia; while among Invertebrates the attempts to trace the pedigree of the Ammonites and Brachiopods are specially noteworthy.

In embryology an important landmark is furnished by **F. M. Balfour's** *Comparative Embryology* (1880–81); in distribution by **A. R. Wallace's** *Geographical Distribution of Animals* (1876), each the first complete treatise on the subject in question. The zoogeographical regions adopted by Wallace were originally proposed by **P. L. Sclater** in 1857. Similar landmarks for Zoology as a whole are **Huxley's** *Anatomy of Vertebrated Animals* (1871) and *Anatomy of Invertebrated Animals* (1877), **Carl Gegenbaur's** *Elements of Comparative Anatomy* (English edition, 1878), **Claus's** *Text-Book of Zoology* (1st English edition, 1884–5), **Ray Lankester's** *Notes on Embryology and Classification* (1877), and the same author's articles in the *Encyclopædia Britannica* (9th edition). Both Claus and Gegenbaur retain Vermes as a primary division; Lankester was the first to split up that unnatural assemblage into distinct phyla, and to include Balanoglossus and the Tunicata among Vertebrates, and Xiphosura and Eurypterida among Arachnida. He also associated Rotifers and Chætopods with Arthropoda, and placed Hirudinea among the Platyhelminthes.

The student who is interested in the permutations and combinations of modern classification may be referred to the works just quoted as well as to the numerous text-books published of late years. The most important point to notice in this connection is the breaking down of the sharp boundaries between the four Cuvierian Branches and a return to something like the conception of unity of type, expressed, however, not as a linear series, but as a

branch-work with the most complex and often puzzling interrelations.

Among the numerous recent contributions to philosophical Zoology it must suffice to mention the works on heredity and kindred subjects of **August Weismann**, the most prominent member of the ultra-Darwinian school, who deny use-inheritance and rely upon natural selection as the main if not the sole factor in evolution. The opposite view, which accepts the truth of use-inheritance, is mainly supported by the American school of Neo-Lamarckians. Weismann has also resuscitated the theory of pre-formation under a modern form. He considers that the various parts of the adult organism are represented in the chromation (germ-plasm) of the sex-cells by ultra-microscopic particles or *determinants*.

In a brief sketch like the present it is impossible to do more than refer, in general terms and without mention of names, to the vast amount of work now being done in every department of Zoology. The output of original research is greater than at any former time and is increasing rapidly, and every important addition to our knowledge necessitates a more or less thorough reconsideration of the general and special problems of morphology and classification. Attention, must, however, be drawn to the researches of the last few years in the departments of experimental and statistical Zoology. Exact observations on comparative physiology, on the precise nature of the action of external conditions, on the physiology of the cell, on the conditions influencing the development and growth of the embryo, and on the limits and characteristics of individual variation, are new fields of study in which it may safely be said that the greatest promise of the future lies.

In conclusion, it must be pointed out that in order adequately to solve the problems of Zoology they must be approached from all sides. From the time of Cuvier to that of Owen comparative anatomy was the dominant branch of the science, and there was a tendency to depreciate the work of the "mere" systematist and outdoor naturalist. For the last five and twenty years embryology has been in the ascendant, and the "mere" anatomist has been somewhat overshadowed. To-day, hopeful signs of a renewed interest in ethology—the study of living animals under natural conditions—are accompanied by a tendency to look upon all laboratory work as necrology rather than biology—the study of corpses rather than of living things. But nothing is more certain than that if the new "natural history" is to be superior to the old—more scientific, more concerned with the solution of general problems—it can only be by utilising to the full all that has been learnt in the laboratory in the departments of anatomy, physiology, and embryology.

APPENDIX

GUIDE TO MODERN ZOOLOGICAL LITERATURE

I. The first essential in the scientific study of Zoology is an acquaintance with the structure of the largest possible number of examples of the chief groups of animals. The following books give directions for dissection and microscopic work: Nos. 1 and 2 will be found to be the most generally useful to the beginner.

1. A. Milnes Marshall. *The Frog: an Introduction to Anatomy, Histology, and Embryology*, 6th edition, 1896.
2. A. Milnes Marshall and C. Herbert Hurst. *Practical Zoology*, 4th edition, 1895. [Amœba, Vorticella, Paramœcium, Hydra, Liver-Fluke, Leech, Earthworm, Crayfish, Cockroach, Fresh-water Mussel, Snail, Amphioxus, Dogfish, Pigeon, Rabbit.]
3. T. H. Huxley and H. N. Martin. *A Course of Practical Instruction in Elementary Biology*, new edition, by G. B. Howes and D. H. Scott, 1888. [Amœba, Vorticella, Paramœcium, Opalina, Hydra, Earthworm, Crayfish, Mussel, Snail, Frog.]
4. G. B. Howes. *Atlas of Practical Elementary Biology*, 1885. [An extensive series of illustrations of the forms described in the preceding work.]
5. T. Jeffery Parker. *A Course of Instruction in Zootomy*, 1884. [Lamprey, Skate, Cod, Lizard, Pigeon, Rabbit.]
6. W. K. Brooks. *Handbook of Invertebrate Zoology*, 1890. [Amœba, Paramœcium, Vorticella, Calcareous Sponge, Zoophyte, Anthomedusa, Leptomedusa, Starfish, Sea-urchin, Embryology and Metamorphosis of Echinoderms, Earthworm, Leech, Crab, Crayfish or Lobster, Metamorphosis of Crab, Cyclops (including metamorphosis), Grasshopper, Mussel, Development of Lamellibranchs, Squid, Development of Squid.]

7. C. Vogt and E. Jung. *Traité d'Anatomie comparee pratique*, 2 vols., 1888–94 (also a German edition). [Amœba, Foraminifer (Polystomella), Actinosphærium, Radiolarian (Actinometra), Paramœcium, Dicyema, Calcareous Sponge, Alcyonium, Aurelia, Hydra, Ctenophore (Bolina), Tænia, Distomum, Turbellarian, Nemertean, Leech, Ascaris, Sipunculus, Rotifer (Brachionus), Earthworm, Lobworm (Arenicola), Feather-star, Starfish, Sea-urchin, Holothurian, Polyzoan (Plumatella), Brachiopod, Mussel, Snail, Pteropod, Cuttle-fish, Crayfish, Centipede, Cockchafer, Spider, Salpa, Simple Ascidian, Amphioxus, Lamprey, Perch, Frog, Lizard, Pigeon, Rabbit.]
8. Burt G. Wilder and S. H. Gage. *Animal Technology* [Cat.]. 3rd edition, 1892.
9. M. Foster and F. M. Balfour. *Elements of Embryology*, new edition, by A. Sedgwick and W. Heape, 1883. [Chick and Rabbit.]

II. Besides the detailed examination of examples of the various groups it is important to know something of the general appearance, habits, etc., of the largest possible number of animals. For this purpose systematic collecting on land, in fresh-water, and by the sea-shore is essential. Zoological gardens and public aquaria should also be visited as well as the zoological department of a well-arranged Museum, in which unknown forms may be identified and the whole subject of classification firmly impressed upon the mind. Special attention should also be directed to the illustrations of general and philosophical zoology to be found in the best modern museums.

There are, however, many rare animals which cannot well be seen alive, and which lose their form and colour when preserved. It is therefore advisable to have access to books illustrated by accurate figures, coloured if possible, of the rarer and less familiar forms. The following works will be found useful from this point of view.

1. Cuvier. *Règne Animal.* Illustrated French edition. No date.
2. Quoy et Gaimard.* *Voyage de Découvertes de l'Astrolabe : Zoologie.*
3. Hombron et Jacquinot. *Voyage au Pol sud et dans l'Océanie : Zoologie.*
4. *Reports of the Scientific Results of the Voyage of H.M.S. Challenger :* "Zoology," 32 vols.
5. *Fauna und Flora des Golfes von Neapel :* 23 vols. already published.
6. The Publications of the Ray Society, especially Carpenter's *Foraminifera*, and Allman's *Gymnoblastic Hydroids* and *Fresh-water Polyzoa.*
7. *Proceedings* and *Transactions of the Zoological Society of London.*
8. R. Lydekker. *The Royal Natural History*, 6 vols., 1894–1896.
9. A. Lister. *The Mycetozoa*, 1894.

10. J. Leidy. *Fresh-water Rhizopoda of North America*, 1879.
11. E. Haeckel. *Die Radiolarien*, 1862.
12. W. Saville Kent. *Manual of the Infusoria*, 3 vols., 1880–81.
13. E. Haeckel. *Die Kalkschwämme*, 3 vols., 1872.
14. W. Hudson and P. H. Gosse. *The Rotifera*, 1889.

III. In making a serious study of Zoology it is essential to have at hand advanced text-books which can be consulted in cases of difficulty, and which give references to the literature of the science, so that the original sources of information can be readily found. The following are the most generally useful to the English student.

1. G. Rolleston and W. Hatchett Jackson. *Forms of Animal Life*, 1888.
2. C. Claus. *Text-book of Zoology*, 2nd English edition, 1890. [Specially useful for finding the zoological positions of unknown animals: brief diagnoses of the groups are given down to families, and the principal genera are named.]
3. E. Ray Lankester and others. Zoological articles contributed to the *Encyclopædia Britannica*, 9th edition, 1891. [Protozoa, Sponges, Hydrozoa, Planarians, Nemertines, Rotifera, Mollusca, Polyzoa, Vertebrata, Tunicata.]
4. C. Gegenbaur. *Elements of Comparative Anatomy*, English Edition, 1878.
5. A. Lang. *Text-book of Comparative Anatomy*, Part I. (Protozoa to Arthropoda), 1891 : Part II. (Mollusca, Echinodermata and Enteropneusta), 1896.
6. R. Wiedersheim. *Elements of the Comparative Anatomy of Vertebrates*, 2nd English edition, adapted by W. N. Parker, 1897.
7. Sir R. Owen. *Anatomy and Physiology of Vertebrates*, 3 vols., 1868.
8. T. H. Huxley. *The Anatomy of Vertebrated Animals*, 1871 : *The Anatomy of Invertebrated Animals*, 1877.
9. A. Günther. *The Study of Fishes*, 1880.
10. Bashford Dean. *Fishes, Living and Fossil*, 1895.
11. A. Willey. *Amphioxus and the Ancestry of the Vertebrates*, 1894.
12. A. Newton. *A Dictionary of Birds*, 1893–96.
13. Sir W. H. Flower. *Osteology of the Mammalia*, 1885.
14. Sir W. H. Flower and R. Lydekker. *Mammals, Living and Extinct*, 1891.
15. *The Cambridge Natural History*, vol. II. (Worms, Rotifers, and Polyzoa), 1896, vol. III. (Mollusca and Brachiopoda), 1895, and vol. V. (Peripatus, Myriapoda, and part of Insecta), 1895, already published.

In addition to the above the following is indispensable for full information.

16. BRONN'S *Klassen und Ordnungen des Thierreichs.* 1859 onwards. The numerous volumes, by various authors, are of very unequal value, some being out of date, others quite recent, others still in progress. The most important are Bütschli's *Protozoa,* Vosmaer's *Porifera,* Chun's *Cœlenterata,* Braun's *Vermes,* Ludwig's *Echinodermata,* Gerstaecker's *Crustacea,* Simroth's *Mollusca,* Hoffmann's *Reptilia,* and Selenka and Gadow's *Aves.*

IV. For special departments of Zoology the following works are recommended.

a. Embryology.

1. KORSCHELT and HEIDER. *Text-book of the Embryology of Invertebrates.* English Edition, 2 vols., 1895–7.
2. F. M. BALFOUR. *A Treatise on Comparative Embryology,* 2 vols., 1880–81.

b. Palæontology.

1. H. ALLEYNE NICHOLSON and R. LYDEKKER. *Manual of Palæontology,* 2 vols., 1889.
2. K. A. VON ZITTEL. *Traité de Paléontologie,* 2 vols., 1887, 1893.

c. Distribution.

1. A. R. WALLACE. *Geographical Distribution of Animals,* 2 vols., 1876; *Island Life,* 1880.
2. A. HEILPRIN. *The Distribution of Animals,* 1887.
3. F. E. BEDDARD. *Text-book of Zoo-geography,* 1895.
4. R. LYDEKKER. *Geographical History of Mammals,* 1896.

c. Philosophy of Zoology.

1. C. DARWIN. *Origin of Species,* 6th edition, 1880; *Descent of Man,* 1882; *Animals and Plants under Domestication,* 2 vols., 1888.
2. G. J. ROMANES. *Darwin and after Darwin,* 2 vols., 1892 and 1895.
3. A. R. WALLACE. *Darwinism,* 1889; *An Examination of Weismannism,* 1893.
4. C. LLOYD MORGAN. *Animal Life and Intelligence,* 1894: *Habit and Instinct,* 1897.
5. A. WEISMANN. *Essays upon Heredity,* 1889 and 1892; *The Germ-Plasm,* 1893.
6. E. B. POULTON. *Colours of Animals,* 1890: *Charles Darwin and the Theory of Natural Selection,* 1896.
7. F. E. BEDDARD. *Animal Coloration,* 1892.
8. O. HERTWIG. *The Biological Problem of To-day,* 1896.

d. History of Zoology.

1. V. CARUS. *Geschichte der Zoologie,* 1872 (French translation, *Histoire de la Zoologie,* 1880).

2. H. F. OSBORN. *From the Greeks to Darwin*, 1894.
3. T. H. HUXLEY. Articles "Biology" and "Evolution," *Encyclopædia Britannica*, 9th edition.
4. E. R. LANKESTER. Art. "Zoology," *ib.*
5. P. GEDDES. Art. "Morphology," *ib.*

V. For the current zoological literature of the day the following periodicals should be consulted.

1. *Journal of the Royal Microscopical Society* Bi-monthly. [Abstracts of the more important papers on Histology, Embryology, and the general Zoology of Invertebrata.]
2. *The Zoological Record.* Annual.
3. *Zoologischer Jahresbericht.* Annual. [Abstracts in German, French, English, or Italian.]
4. *Zoologischer Anzeiger.* Fortnightly [Complete current bibliography.]
5. *Zoologisches Centralblatt.* Fortnightly. [Critical abstracts of current publications.]
6. *Biologisches Centralblatt.* Fortnightly. [Contains, in addition to original articles, *résumés* of recent publications.]
7. *Anatomischer Anzeiger.* [Complete current bibliography.]
8. *Natural Science.* Monthly.

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